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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 107, NO. 1 MARCH 1995 PAGES 1–192

(ISSN 0043-5643)

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FOUNDED DECEMBER 3, 1888

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THE WILSON BULLETIN
(ISSN 0043-5643)

THE WILSON BULLETIN (ISSN 0043-5643) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Second-class postage paid at Lawrence, KS. POSTMASTER: Send address changes to THE WILSON BULLETIN, P.O. Box 1897, Lawrence, KS 66044-8897.

Back issues or single copies are available for $12.00 each. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

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Glaucidium parkeri sp. nov. and the Least Pygmy-Owl (*Glaucidium minutissimum*) complex. 1: *G. palmarum* (Colima Pygmy-Owl); DMNH 23956. 2: *G. sanchezi* (Tamaulipas Pygmy-Owl; female on left, male on right); DMNH 52842, 52843. 3: *G. griseiceps* (Central American Pygmy-Owl; purple circles indicate apparently disjunct populations); LSUMZ 80177. 4: *G. parkeri* sp. nov. (Subtropical Pygmy-Owl; black circles indicate specific localities); ANSP 185160. 5: *G. hardyi* (Amazonian Pygmy-Owl; sonogram courtesy of J. W. Hardy and ARA records); LSUMZ 132017. 6: *G. minutissimum* (Brazilian Pygmy-Owl); FMNH 302147. Painting by Sophie Webb.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 107, NO. 1 MARCH 1995 PAGES 1–192

Wilson Bull., 107(1), 1995, pp. 1–6

A NEW SPECIES OF PYGMY-OWL (STRIGIDAE: *GLAUCIDIUM*) FROM THE EASTERN ANDES

MARK B. ROBBINS[1] AND STEVE N.G. HOWELL[2]

ABSTRACT.—A new species of pygmy-owl (*Glaucidium parkeri* sp. nov.) from the eastern slope of the eastern Andes of Ecuador and Peru is described. This subcanopy dwelling species appears to be uncommon in subtropical forest on outlying ridges of the main Andean chain between 1450 and 1975 m elevation. Plumage and vocalizations indicate that it is allied to the Least Pygmy-Owl (*G. minutissimum*) complex. *Received 8 Nov. 1993, accepted 8 May 1994.*

In 1969 and 1970, John Weske and John Terborgh mist-netted two pygmy-owls along the eastern slope of the Andes in central Peru (Deptos. Ayacucho and Huánuco) that were identified as *Glaucidium minutissimum* based on their small size. Nearly three years ago, during the initial stages of our revision of the *Glaucidium minutissimum* complex (Howell and Robbins 1995), we independently examined these specimens in the American Museum of Natural History (AMNH 820933, 820647) and concluded that they represented an undescribed taxon. Aside from the data on the specimen labels, nothing was known about this taxon until Bret Whitney sent us a tape recording that he made on 21 January 1991 of a probable *G. minutissimum* at 1660 m on the lower slopes of Volcán Sumaco, Prov. Napo, Ecuador. When Robbins listened to Whitney's tape, he realized that birds he had tape recorded between 1700 and 1975 m in the Cordillera de Cutucú (Library of Natural Sounds, Cornell Laboratory of Ornithology, #41504; Robbins et al. 1987), and originally identified as *G. jardinii*, were referable to the same species as in the Whitney recording.

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Given the elevational range and distribution of the above records we strongly suspected that the Peruvian specimens and the vocalizations of the Ecuadorian birds represented the same undescribed taxon. Confirmation of this was finally obtained when Francisco Sornoza Molina, while conducting avifaunal inventory work for the Academy of Natural Sciences of Philadelphia (ANSP) and the Museo Ecuatoriano de Ciencias Naturales, Quito (MECN), tape recorded and collected a *Glaucidium* from ca 20 m up in the subcanopy of a tree on 22 July 1992 at 1600 m in southeastern Ecuador (Prov. Zamora-Chinchipe; 04°37′S, 78°58′W). Sornoza's specimen (ANSP 185160) clearly is referable to the same species as the Weske and Terborgh specimens, and the vocalizations that he procured are like those of the Whitney and Robbins' recordings. We propose to name this distinctive new pygmy-owl

Glaucidium parkeri sp. nov.
Subtropical Pygmy-Owl

HOLOTYPE.—Academy of Natural Sciences of Philadelphia, No. 185160; adult male (testes 6.0 × 3.5 mm; no bursa), Ecuador: Prov. Zamora-Chinchipe; Panguri, ca 12 km NE San Francisco del Vergel, 04°37′S, 78°58′W, elevation 1600 m; 22 July 1992; collected by F. Sornoza Molina. Recordings of voice deposited at the Library of Natural Sounds, Cornell Laboratory of Ornithology (LNS #63426).

DIAGNOSIS.—Its small size, unmarked mantle, song, and ecological requirements clearly place *parkeri* within the *G. minutissimum* complex (includes *G. griseiceps, G. hardyi, G. minutissimum, G. palmarum,* and *G. sanchezi*; Howell and Robbins, 1995). In plumage, *parkeri* is the most distinctive member of the complex: distinguished from all members of the complex by the relatively large and distinct white crown and scapular and upper wing covert spots (see frontispiece). Banding (irregular shaped white spots) on the wings, unlike the buffy bands in all other members of the complex. Dorsum, upper chest, and the ventral streaks are less rufous than in all other taxa of the *minutissimum* complex.

DESCRIPTION OF HOLOTYPE.—Capitalized color descriptions and numbers follow Smithe (1975, 1981). Crown grayish-brown (closest to Hair Brown 119A but with a distinct grayish tone). Entire pileum and sides of face with conspicuous white spots bordered with dark brown (Sepia 119). Concealed white nuchal collar. Back, scapulars, upper wing coverts, and rump dark brown (closest to Sepia 219) with dull olivaceous-rufous wash, to outer edge of wing coverts and secondaries. Scapulars and upper wing coverts with bold white spots. Primaries and secondaries darker than dorsum (closest to Sepia 119), with conspicuous, irregularly shaped white spots on the outer webs and concealed, larger white spots on the inner webs. Tail blackish (closest to Sepia 119) with five incomplete white bands that appear as irregularly shaped spots. Underparts, from chin to crissum, white. Throat feathers tipped apically with dark brown (closest to Sepia 219). Sides of chest medium brown (closest to Hair Brown 119A) with a few inconspicuous white spots. Broad, ill-defined dull olivaceous rufous-brown (closest to Hair Brown 119A, but with dull olive-rufous wash) streaks on lower chest, flanks, and abdomen. Soft part colors: irides yellow; bill greenish-yellow; toes yellow.

MEASUREMENTS OF HOLOTYPE—Wing (chord) 91.8 mm, tail 48.5 mm, bill (from cere) 11.2 mm, mass 62 g.

ETYMOLOGY—We take great pleasure in naming this new owl in honor of the late Theodore A. Parker, III who for over twenty years accumulated an unparalleled knowledge

of Neotropical birds and graciously shared his vast expertise with all. Robbins, and a number of the people who contributed vocal material and information to this and the subsequent paper, owe special gratitude to Ted for his friendship and encouragement throughout their Neotropical careers.

SPECIMENS EXAMINED.—The taxonomy that follows is documented in Howell and Robbins (1995). The following list is of specimens (N = 151) that we examined. In addition to the material listed below, we received morphometric data for three *G. griseiceps* from Costa Rica, and four *G. minutissimum* and one *G. hardyi* from Brazil (see acknowledgments).

Glaucidium parkeri: type locality; Peru: Depto. Huánuco; Cerros del Sira, 09°25′S, 74°44′W, elevation 1550 m (AMNH 1 male); Depto. Ayacucho; Huanhuachay, 12°43′S, 73°47′W, elevation 1660 m (AMNH 1 male).

Glaucidium palmarum: all from Mexico. Sonora: Mirasol (LSUMZ 11 males, 3 females; WFVZ 6 males, 2 females; DMNH 1 male); El Aguaji, Quintero (DMNH 1 male); Sierra Taramaru, Guirocoba (LSUMZ 1 female); Sinaloa: San Miguel (MLZ 1 male, 1 female); NE Rosario (MLZ 1 male); Cacalotan (MLZ 1 female); Cosala (MLZ 3 males); Nayarit: San Blas (LSUMZ 1 female; DMNH 1 male, 1 female); Chacala (MLZ 2 males); Las Varas (MLZ 1 male; DMNH 3 males, 1 female); E Compostela (DMNH 1 female); Tepic (DMNH 1 male); S Santiago (MLZ 1 male, 1 female); Santa Teresa (MLZ 1 male); Jalisco: SSW Autlán (WFVZ 4 males, LSUMZ 4 males, DMNH 1 male, 1 female); S Puerto Vallarta (DMNH 2 males); Suchitlán (DMNH 2 males, 1 female); Colima: Tecolapa (LSUMZ 1 male); Cerro Chino (LSUMZ 5 males; WFVZ 1 male; Pueblo Juarez (LSUMZ 4 males, WFVZ 2 males, 1 female; DMNH 3 males, 1 female); Pueblo Nuevo (DMNH 2 males); S Colima (WFVZ 2 males); Guerrero: El Naranjo (USNM 1 male); Zirandaro (MLZ 1 male, 1 female); Mexcala (MLZ 1 male, 3 females); Oaxaca: Puerto Escondido (LSUMZ 7 males); Morelos: Xicatlacotla (MLZ 2 males); E Cuernavaca (WFVZ 1 male, DMNH 1 male).

Glaucidium sanchezi: all from Mexico. Tamaulipas: NW Gomez Farias, Rancho del Cielo (BMNH 2 males; DMNH 1 male, 4 females); San Luis Potosí: Cerro Coneja (LSUMZ 3 males, 1 female); Cerro San Antonio (LSUMZ 1 male); Xilitla (LSUMZ 1 male).

Glaucidium griseiceps: Mexico: Tabasco; S Chontalapa (LSUMZ 1 male); SW Ocuápan (LSUMZ 1 male); Oaxaca; Valle Nacional (LSUMZ 1 male); Piedra Blanca (AMNH 1 male); Chiapas; Palenque (MLZ 1 male); Guatemala: no locality (USNM 2 unsexed; FMNH 1 unsexed); Honduras: Lake Yojoa (CMNH 1 male); Panama: Panama; Peluca (USNM 1 male); Darién; mouth Río Tuquesa (USNM 1 male); Cerro Tacarcuna (LSUMZ 1 female); Colombia: Socarré, Río Sinú (USNM 1 male).

Glaucidium hardyi: Peru: Depto. Ucayali; Río Curanja, Balta (LSUMZ 1 female); Depto. Madre de Dios; Río Tambopata, Collpa (FMNH 1 male); Bolivia: Depto. Pando, Cobija (LSUMZ 2 males); Brazil: Río Solimões, Caviana (CMNH 2 males); Rondônia; Cachoeiva Nazaré, Río Jiparana (FMNH 1 male).

Glaucidium minutissimum: Brazil: "interior state of Bahía", (AMNH syntypes 2 unsexed); São Paulo (FMNH 1 male); no locality, (AMNH 1 male, 1 female, 1 unsexed; ANSP 1 male, 4 unsexed; USNM 1 unsexed; FMNH 1 unsexed).

VOCALIZATIONS EXAMINED.—All localities represent a single bird unless otherwise noted in parentheses. Three of the following recordings are from Hardy et al. (1990).

Glaucidium parkeri: Ecuador: Prov. Napo, Volcán Sumaco; Prov. Morona-Santiago, W slope Cord. de Cutucú (2) and Cord. del Condor, Coangos; Prov. Zamora-Chinchipe, Panguri.

Glaucidium palmarum: all from Mexico. Sinaloa: NW Villa Union (2); Jalisco: N Barra de Navidad; Colima: Colima-Minatitlan Road; SE Cuidad Colima; Morelos: ESE Cuernavaca.

Glaucidium sanchezi: all from Mexico. Tamaulipas: Rancho del Cielo (5); San Luis Potosí: W El Naranjo (4).

Glaucidium griseiceps: Mexico: Veracruz, Uxpanapa; Oaxaca, S Valle Nacional; Chiapas, Palenque; Belize: W Gallon Jug (2); Guatemala: Depto. Peten, Tikal; Depto. Isabal, Cerro San Gil; Depto. Retalhuleu; Costa Rica: Braulio Carrillo National Park (2); Prov. Limon, Cahuita National Park; Panama: Prov. San Blas, "Nusagandi"; Darién, Cerro Pirre (3); Colombia: Chocó, Parque Nacional Los Katíos; Ecuador: Prov. Esmeraldas, NW Alto Tambo (2).

Glaucidium minutissimum: all from Brazil. São Paulo, Bissucanga; Espírito Santo, Linhares; Bahia, Boa Nova.

Glaucidium hardyi: Brazil: Rondônia, Jiparana.

REMARKS

Individual variation.—The two male Peruvian specimens of *G. parkeri* virtually are indistinguishable, and these two vary only slightly in plumage from the male holotype from southeastern Ecuador. The holotype is slightly darker, with even less of a rufous brown tinge to the dorsum and the streaking on the ventral surface, than the two Peruvian males. In addition to the diagnostic plumage characters, *G. parkeri* may be distinguished from its two geographically closest relatives, the recently described Amazonian Pygmy-Owl (*G. hardyi*) (Vielliard 1989) and the widespread Central and Pacific-slope South American *G. griseiceps* (Howell and Robbins 1995) by morphometrics. Male *G. parkeri,* on average, are heavier than male *G. hardyi* (two-tailed *t*-test, $P < 0.05$; Table 1 in Howell and Robbins 1995). *Parkeri* averages shorter in wings and is heavier than male *G. griseiceps* (two-tailed, *t*-test,. $P < 0.05$, $P < 0.01$, respectively; table 1 in Howell and Robbins 1995).

Song.—The song of *G. parkeri* is typically three notes (range 2–4 notes/song) and is characterized by a consistent increase in the length of the inter-note interval (vs a more-or-less regular pacing in other forms with songs of three or more notes). This is most pronounced between the final two notes and gives the effect of a hesitation before the last note of each song; this is unique among New World *Glaucidium* (Howell and Robbins 1995).

Distribution.—In addition to the localities listed above, *G. parkeri* was found by its namesake and Jaqueline Goerck at an Ecuadorian military camp, Coangos, near the northern end of the Cordillera del Condor, Prov. Morona-Santiago, on 20 July 1993 (ca 03°29′S, 78°14′W). A single bird responded to *Glaucidium* imitations by Parker between 08:00 and 08:15 h at 1450 m. It perched on a bare branch of a tall tree over 30 m above the ground.

The elevational ranges of *G. parkeri* and *G. sanchezi* are unique within the *G. minutissimum* complex (Howell and Robbins 1995). With the exception of the northeastern Mexican *G. sanchezi,* all records of *par-*

keri, 1450–1975 m (N = 6 localities), are above the upper elevational records of other members of the *G. minutissimum* complex. *Glaucidium palmarum* has been recorded as high as 1500 m in dry, pine-oak woodland of western Mexico (Buchanan 1964), *G. griseiceps* has been recorded in humid evergreen forest up to ca 1300 m in Oaxaca, Mexico (Binford 1989; Howell, pers. obs.), on the Pacific slope of Guatemala (B. Whitney, tape recording), and ca 1000 m at Cerro Pirre, Darién, Panama (Robbins et al. 1985). *G. minutissimum* has been recorded in evergreen forest up to 1000 m in eastern São Paulo, Brazil (D. Stotz, pers. comm.).

The Andean Pygmy-Owl (*G. jardinii*) replaces *G. parkeri* above ca 2000 m on the eastern slope of the Andes. The lower elevational range of *parkeri* remains to be ascertained, but we do not believe that it is determined through competitive exclusion by congeners. *Glaucidium hardyi* has not been recorded above ca 350 m, and it is unknown from Colombia, Ecuador, and north of the Río Amazonas and west of the Río Ucayali drainage in Peru (König 1991; T. Parker, pers. comm.; LSUMZ, unpubl. data). Moreover, given that *hardyi* and the Ferruginous Pygmy-Owl (*G. brasilianum*) broadly overlap in range and are quite divergent in habitat preferences, we suspect that there would be no exclusion between the distantly related *parkeri* and *brasilianum* if they should meet in the Andean foothills. Because it is restricted to humid subtropical forest, *parkeri* would not contact the recently described *G. peruanum* (König 1991), because the latter species is found only in arid montane forest and deserts of Chile, Peru, and western and southern Ecuador.

All six *G. parkeri* localities are on outlying ridges from the main Andean chain. It is conceivable that *parkeri,* like other taxa that appear to be found only on semi-isolated ridges (e.g., *Heliangelus regalis, Hemitriccus cinnamomeipectus,* Fitzpatrick et al. 1979, Fitzpatrick and O'Neill 1979, respectively), may be restricted to such ridges. We predict that *parkeri* will be found at least as far north as southeastern Colombia.

ACKNOWLEDGMENTS

We express our gratitude to a number of first-rate field observers who have generously shared their pygmy-owl tape recordings with us. They include John C. Arvin, Robert A. Behrstock, Paul Coopmans, Jeff Kingery, Greg W. Lasley, Theodore A. Parker, III, Gary H. Rosenberg, Francisco Sornoza M., F. Gary Stiles, Bret M. Whitney, and David Wolf. Greg Budney and the Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York, provided material from their sound collection. Luis F. Batista kindly made available his sound analysis laboratory at the California Academy of Sciences and offered helpful comments on spectrogram interpretation. We are indebted to Jaqueline Goerck for making available Ted Parker's notes and recordings. Doug Stotz, Mario Cohn-Haft, and Rafael G. Campos R. provided data from Brazilian and Costa Rican pygmy-owl specimens, respectively. Ned K. Johnson made valuable comments on the manuscript.

We are grateful to the following institutions and people for loaning us specimens (listed in alphabetical order by institution): Mary LeCroy (American Museum of Natural History [AMNH]); Gary Voelker (Bell Museum of Natural History, Univ. of Minnesota [BMNH]); Kenneth Parkes (Carnegie Museum of Natural History [CMNH]); Gene Hess (Delaware Museum of Natural History [DMHH]); Scott Lanyon and David Willard (Field Museum of Natural History [FMNH]); Van Remsen and Steve Cardiff (Louisiana State Museum of Natural Science [LSUMZ]); John Hafner (Moore Laboratory of Zoology, Occidental College [MLZ]); Gary Graves (National Museum of Natural History, Smithsonian Institution [USNM]); and Lloyd Kiff (Western Foundation of Vertebrate Zoology [WFVZ]).

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COLOR PLATE

Publication of the frontispiece painting by Sophie Webb has been made possible by an endowment established by George Miksch Sutton.

Wilson Bull., 107(1), 1995, pp. 7–25

SPECIES LIMITS OF THE LEAST PYGMY-OWL (*GLAUCIDIUM MINUTISSIMUM*) COMPLEX

Steve N. G. Howell[1] and Mark B. Robbins[2]

Abstract.—The Least Pygmy-Owl (*Glaucidium minutissimum*) complex comprises 10 described taxa that inhabit tropical and subtropical forests. Consistent song differences among taxa in this complex, supported by morphometric, plumage, and habitat data, indicate that, in addition to the recently described *G. hardyi* and *G. parkeri*, four species can be recognized in the Least Pygmy-Owl complex: *G. palmarum* of western Mexico (includes the described subspecies *palmarum, oberholseri,* and *griscomi*); *G. sanchezi* of northeastern Mexico; *G. griseiceps* of southeastern Mexico, Central America, and the Pacific slope of northern South America (includes the described subspecies *griseiceps, rarum,* and *occultum*); and *G. minutissimum* of southeastern Brazil and adjacent Paraguay. *Received 8 Nov. 1993, accepted 9 May 1994.*

The genus *Glaucidium* comprises a number of species of small owls widespread in the Americas, Eurasia, and Africa. Four groups of mainland New World *Glaucidium* are generally recognized: the *G. gnoma* complex (western Canada to Honduras), the *G. brasilianum* complex (southwestern United States to southern South America), the *G. minutissimum* complex (Mexico to South America), and the *G. jardinii* complex (Costa Rica to South America) (Peters 1940, Meyer de Schauensee 1970, A.O.U. 1983, Sibley and Monroe 1990). Although the *G. brasilianum* complex stands out as relatively distinct by virtue of its streaked crown and proportionately longer tail with numerous pale bars, differences between the spotted-crowned *gnoma* and *jardinii* groups and the *minutissimum* group have been confused (e.g., Griscom 1931, König 1991). The *G. minutissimum* (Least Pygmy-Owl) complex comprises the spotted-crowned pygmy-owls of tropical and subtropical forests, distinguished from the *gnoma* and *jardinii* groups of temperate forest habitats by their smaller size and unmarked backs.

TAXONOMIC HISTORY

Until recently, *G. minutissimum* was considered a polytypic species (with eight described subspecies) ranging from both slopes of Mexico to northern Bolivia, Paraguay, and southeastern Brazil (Peters 1940, Meyer de Schauensee 1970, A.O.U. 1983, Parker and Remsen 1987). This traditional taxonomic classification relied heavily on plumage and morphology which, particularly in nightbirds, can be remarkably uniform within genera. The increasing realization that vocalizations are important in unmasking morphologically cryptic species

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was largely responsible for the description of two distinct new species in the *G. minutissimum* complex: *G. hardyi* (Amazonian Pygmy-Owl) (Vielliard 1989) and *G. parkeri* (Subtropical Pygmy-Owl) (Robbins and Howell 1995). König (1991) believed that *G. hardyi* was not part of the *G. minutissimum* complex but is more closely related to the *G. jardinii* complex; he based this on the vocal characters of these taxa. We believe, however, based on plumage pattern, size, biogeography, habitat preferences, and an understanding of the vocal range of all forms involved, that *G. hardyi* is allied to the *G. minutissimum* complex.

Buchanan (1964) clarified much of the confusion that had surrounded the identification and taxonomy of Least Pygmy-Owls in Mexico, in particular pointing out that they do not possess dichromatic plumage commonly associated with other *Glaucidium.* He recognized that Mexican Least Pygmy-Owls were divisible into two natural groups which coincided with biogeographic areas: dark, richly colored birds, ranging from eastern and southern Mexico to South America, and light, dull colored birds in western Mexico. Buchanan (1964) also noted the "contrasting ecological circumstances" of western versus eastern forms and that the two groups might represent separate species. In conclusion, however, he opted for a conservative approach and retained all forms as members of a single species. The A.O.U. (1983) commented that "populations on the Pacific slope of Mexico may constitute a distinct species" and that "Further study of this complex is required to determine relationships."

We have gathered vocal, morphological, and ecological data that dictate a revision of the *G. minutissimum* complex. In addition to the recently described *G. hardyi* and *G. parkeri,* we recognize four species in the Least Pygmy-Owl complex: *G. palmarum* of western Mexico (includes the described subspecies *palmarum, oberholseri,* and *griscomi*); *G. sanchezi* of northeastern Mexico; *G. griseiceps* of southeastern Mexico, Central America, and the Pacific slope of northern South America (includes the described subspecies *griseiceps, rarum,* and *occultum*); and *G. minutissimum* of southeastern Brazil and adjacent Paraguay.

METHODS

We listened to and analyzed tape recordings of a total of 555 songs of 37 individuals from throughout the range of the *minutissimum* complex, with the exception of *G. hardyi,* whose distinctive song was discussed by Vielliard (1989). These included songs of all described taxa: 40 songs of *G. palmarum,* 130 of *G. sanchezi,* 155 of *G. griseiceps,* 160 of *G. parkeri,* and 70 of *G. minutissimum.* Voice showed little or no significant difference among the described races of *palmarum* and *griseiceps,* and we pooled samples of the respective subspecies for between-species analyses. Recordings were analyzed by Howell using a Kay Elemetrics DSP Sonograph, Model 5500. Dominant frequency was determined from a power spectrum (amplitude [dB] plotted against frequency [Hz]). Analysis of variance (ANOVA) was used to test for significance levels in song characters.

For morphological analysis we examined 151 specimens (148 assembled at ANSP) of all ten described taxa of the *G. minutissimum* complex, representing virtually all specimens (including the syntypes of *G. minutissimum* and *G. sanchezi* and the holotype of *G. parkeri*) in North American collections (see Robbins and Howell [1995] for a list of specimens examined). In addition, morphometric data from several specimens in foreign institutions (see acknowledgments) and the literature were used in our analysis. Because plumage and morphology showed at best minor differences among the described subspecies of *G. palmarum* and *G. griseiceps,* we pooled samples of the respective subspecies for measurements, which were made by Robbins to the nearest 0.1 mm using dial calipers.

RESULTS

Voice.—The primary songs of the five members of the Least Pygmy-Owl complex discussed below consist of a variable number of hollow,

single-note whistles, or hoots, which are given in bouts that may last for long periods. In addition, *G. palmarum, G. sanchezi, G. griseiceps,* and *G. minutissimum* give a soft, quavering trill that may be repeated up to a few times in succession and which often precedes bouts of hooting; we have not heard a comparable vocalization from *G. parkeri.* The primary song of the sixth species, *G. hardyi,* is a rapid series of short notes run into a quavering roll or trill (Hardy et al. 1990; Frontispiece) and was discussed by Vielliard (1989). This trill is relatively loud and ringing and is not analogous to the soft trills given by other members of the complex; the latter tend to be given by birds in an agitated state, such as when counter-singing or in response to voice playback. The four song characters we examined were frequency (or pitch), duration of notes in a song, duration of intervals between notes in a song (inter-note intervals), and inter-song intervals (Table 1). Frequency, note duration, and inter-note interval were fairly consistent for an individual bird. Inter-song interval was more variable, although some significant inter-specific differences in singing rate were apparent.

The mean dominant frequency varied between 1278 Hz (*parkeri*) and 1483 Hz (*sanchezi*), and within-taxon variation in mean ranged from 92 Hz (*minutissimum*) to 304 Hz (*griseiceps*) (Table 1). The variation in mean for *griseiceps* may seem large, but this species has a large geographic range. Further, Galeotti et al. (1993) showed a variation of 201 Hz (1343–1544 Hz) in the mean fundamental frequency (comparable to the dominant frequency) in ten males in a localized population of the Eurasian Pygmy-Owl (*G. passerinum*). Thus, while song frequency varies among taxa in the *G. minutissimum* complex (e.g., *sanchezi* is significantly higher pitched than all other taxa; $P < 0.05$), frequency may be more important overall for individual than for specific recognition.

The most obvious differences to the human ear among the songs of species in the *G. minutissimum* complex are the different tempos and the varying number and duration of notes which give each species its distinctive song. That both the mean frequency and note duration (0.22–0.29 s; Galeotti et al. 1993) of *G. passerinum* overlap with members of the *G. minutissimum* complex (see above and Table 1) suggests that the number and structure of notes, in combination with the overall tempo, may be the most important taxonomic aspects of *Glaucidium* vocalizations. Further support for the taxonomic value of tempo and number of notes may be found by comparing Example 1 of *G. brasilianum* (Hardy et al. 1990) with *G. palmarum.* The former has short, arched notes of 0.09–0.10 s separated by 0.30 s pauses, and a dominant frequency of 1460 Hz. Other than a steady pacing between the first three notes and more prolonged hooting overall, this bird's song appears spectrographically indistinguish-

TABLE 1

MEAN (±SD) AND RANGE FOR SELECTED SONG CHARACTERS OF THE (*GLAUCIDIUM MINUTISSIMUM*) COMPLEX

	Mean dominant frequency (Hz)	Length of notes (s)	First inter-note interval (s)	Second inter-note interval (s)	Mean inter-song interval (s)
G. palmarum	1416 (±61.1) (1300–1465[a]) N = 6/38[c]	0.10 (±0.02) (0.09–0.14[b]) N = 6/78[c]	0.34 (±0.03) (0.29–0.39[b]) N = 6/13[c]	0.31 (±0.03) (0.26–0.34[b]) N = 6/13[c]	4.8 (±1.61) (2.6–5.9[a]) N = 6/33[c]
G. sanchezi	1483 (±41.8) (1390–1540) N = 9/56	0.26 (±0.03) (0.21–0.30) N = 9/106	0.43 (±0.04) (0.32–0.52) N = 9/45	0.43 (±0.04) (0.38–0.47) N = 2/6	5.2 (±0.73) (4.3–6.5) N = 9/100
G. griseiceps	1385 (±94.1) (1232–1536) N = 14/92	0.14 (±0.04) (0.09–0.23) N = 13/148	0.23 (±0.04) (0.18–0.33) N = 12/28	0.22 (±0.03) (0.17–0.29) N = 12/28	7.3 (±3.70) (3.2–13.1) N = 12/75
G. parkeri	1278 (±152.2) (1160–1450) N = 3/52	0.15 (±0.03) (0.10–0.22) N = 3/123	0.18 (±0.04) (0.10–0.25) N = 3/37	0.26 (±0.06) (0.15–0.37) N = 3/37	2.3 (±0.96) (1.2–3.0) N = 3/90
G. minutissimum	1358 (±35.7) (1320–1412) N = 5/44	0.26 (±0.03) (0.21–0.32) N = 5/93	0.28 (±0.04) (0.22–0.34) N = 5/37	0.26 (±0.01) (0.25–0.30) N = 1/11	7.0 (±2.15) (3.2–8.2) N = 5/50

[a] Range of individual means.
[b] Range of total number of notes or intervals.
[c] Number of birds/number of notes or intervals.

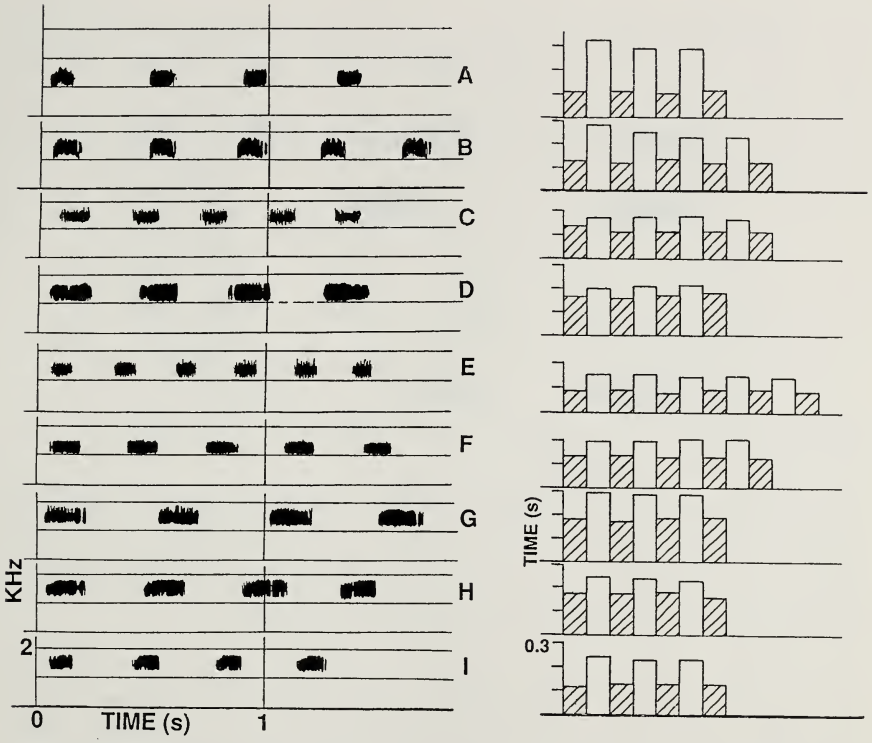

FIG. 1. Spectrograms and histograms of the songs of *Glaucidium palmarum* (A–B) and *G. griseiceps* (C–I) all to the same scale. In histograms, shaded bars represent notes, unshaded bars represent inter-note pauses. In *palmarum,* the short notes are often arched and are separated by relatively long pauses that are 1.9–3.6 × longer than the notes, with the longest pause between the first and second notes. In *griseiceps,* the notes within a song are overall equal in duration and are paced steadily with pauses 1.1–2.0 × the length of the notes. A: *G. p. palmarum.* Microondas La Cumbre, Colima, Mexico. Apr 1988 (Howell). B: *G. p. griscomi.* Cañon de Lobos, Morelos, Mexico. Jun 1991 (Howell). C: *G. g.* "*occultum*". Uxpanapa, Veracruz, Mexico. Jan 1992 (Howell). D: *G. g. griseiceps.* Gallon Jug, Belize. May 1992 (Whitney). E: *G. g. griseiceps.* Cerro San Gil, Izabal, Guatemala. Feb 1991 (Howell). F: *G. g.* "*rarum*". Braulio Carillo, Costa Rica. Apr 1982 (Wolf). G: *G. g.* "*rarum*". Nusagandi, San Blas, Panama. Feb 1987 (Whitney). H, I: *G. g.* "*rarum*?". Alto Tambo, Esmeraldas, Ecuador, Jul 1990 (Robbins).

able from that of *palmarum* and is thus more similar to it than are other members of the *G. minutissimum* complex.

G. palmarum: songs comprise 2–24 short hoots separated by long pauses (Table 1, Fig. 1A–B). The first inter-note interval is significantly longer than the second ($P < 0.05$), after which the pacing is fairly steady, although intervals between notes often decrease slightly overall throughout

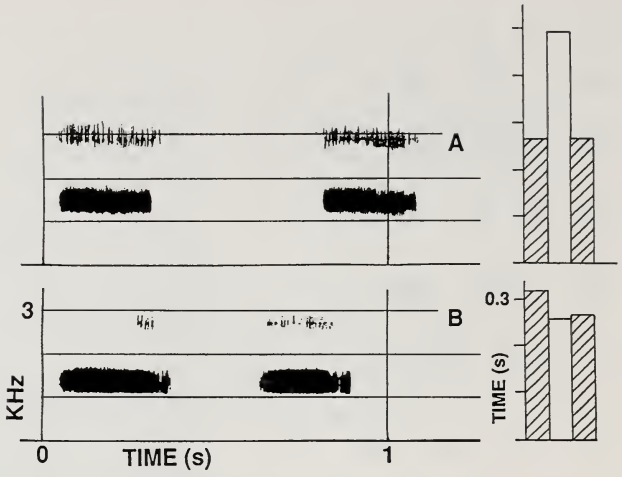

FIG. 2. Spectrograms and histograms (see Fig. 1 for key) of typical songs of *Glaucidium sanchezi* (A) and *G. minutissimum* (B) to same scale. The higher-pitched *sanchezi* has a significantly longer pause between notes, and the second note of *minutissimum* is consistently shorter than the first. A: Rancho del Cielo, Tamaulipas, Jun 1985 (Arvin). B: Floresta Río Doce forest reserve, Espírito Santo, Brazil, Oct 1991 (Whitney).

the song (Fig. 1A–B). The song bouts often begin with two and three-note songs and build up to the commonly given six to 10-note songs; usually when songs reach 6–8 hoots they vary, seemingly randomly, in their number of notes. The first few notes, and sometimes all notes in a song, are arched, contributing to a hollow, wooden to slightly plaintive quality that suggests the Ferruginous Pygmy-Owl (*G. brasilianum*).

Within the *minutissimum* complex, the song of *palmarum* appears closest to *G. griseiceps* from which it is distinguished by its short notes separated by longer intervals (Fig. 1A–B vs 1C–I; Table 1), with the first inter-note interval longest. The difference in tempo between these two species is reflected by the difference between inter-note interval and note duration being significantly greater in *palmarum* than in all populations of *griseiceps* ($P < 0.001$). Also, inter-song interval is significantly shorter in *G. palmarum* than in *G. griseiceps* ($P < 0.05$). *Palmarum* differs from *G. sanchezi* and *G. minutissimum* in its long songs of short notes (Table 1; and compare Figs. 1A–B and 2A–B), and from *G. parkeri* in its longer, steadier-paced songs of short notes, with the first inter-note interval longest, and significantly longer inter-song intervals ($P < 0.05$) (Table 1; compare Figs. 1A–B and Fig. 3).

G. sanchezi: songs comprise 1–3 slow-paced, high-pitched, long hoots with a long pause between them (Table 1; Fig. 2A). Two-note songs

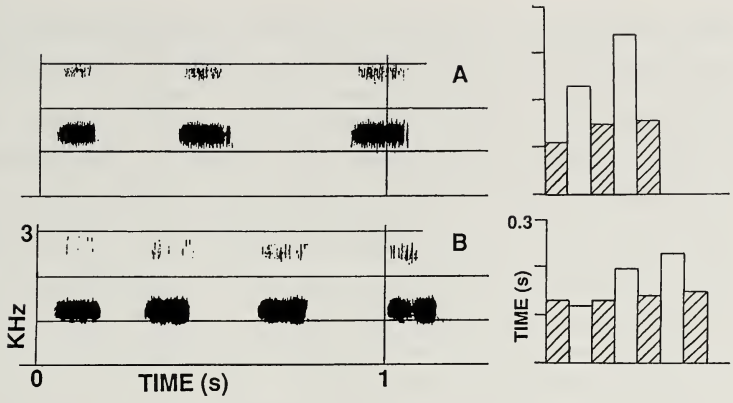

FIG. 3. Spectrograms and histograms (see Fig. 1 for key) of typical songs of *Glaucidium parkeri* to same scale. This species has successively increasing pauses between notes and, to a lesser extent, increasing duration of notes. A: three-note song, 04°37′S, 78°58′W, Prov. Zamora-Chinchipe, Ecuador. July 1992 (Sornoza). B: four-note song, Volcán Sumaco, Prov. Napo, Ecuador. Jan. 1991 (Whitney).

appear commonest, but two and three-note songs may be repeated and alternated, seemingly at random, and single-note songs (apparently unique in this complex) also may be repeated steadily.

The song of *sanchezi* is strikingly different from those of *G. palmarum, G. griseiceps,* and *G. parkeri* by virtue of its long notes and inter-note intervals, and number of notes (Table 1; Figs. 1–3), and it sounds superficially similar to the song of the geographically distant *G. minutissimum.* The song of *sanchezi* is slower-paced, however, because the inter-note interval of *sanchezi* is highly significantly longer than *minutissimum* ($P < 0.001$; Table 1). Thus the inter-note interval of *sanchezi* is 0.03–0.23 s longer ($\bar{x} = 0.15$ s $\pm$ 0.06; N = 21, 2-note songs) than the longest note, vs 0.10 s longer or shorter ($\bar{x} = -0.01$ s $\pm$ 0.06; N = 26, 2-note songs) in *minutissimum.* Also, the second note of a two-note *minutissimum* song is significantly shorter than the first ($P < 0.05$), whereas in *sanchezi* the second note of a two-note song is not significantly different from the first (0.03 s shorter to 0.05 s longer) (Fig. 2). Further differences are the significantly higher frequency of *sanchezi* vs *minutissimum* ($P < 0.001$) and the significantly shorter inter-song interval of *sanchezi* ($P < 0.05$), which helps separate the singing tempo of these two species.

Of interest is the geographic variation apparent between two disjunct populations of *G. sanchezi* that have been tape recorded. Thus, birds at Rancho del Cielo in Tamaulipas give significantly longer notes ($\bar{x} = 0.28$ s $\pm$ 0.01, N = 5 birds) than birds west of El Naranjo in San Luis Potosí

($\bar{x}$ = 0.24 s ± 0.02, N = 4 birds) ($P < 0.001$). In all other respects (noted above), the songs of these populations are similar to one another and differ consistently from all other species in the complex.

G. griseiceps: songs comprise 2–18 hoots of variable duration (Table 1). Like *G. palmarum,* the song bouts of *G. griseiceps* often begin with two and three-note songs and build up to the commonly given six to 10-note songs which then vary, seemingly randomly, in their number of notes. The song has a ringing, slightly bell-like quality, quite different from *palmarum* and would not be mistaken for a Ferruginous Pygmy-Owl. Despite geographic variation (see below), consistent features of the song of *G. griseiceps* are the overall steady pacing between notes, reflected by no significant difference between first and second inter-note intervals (vs shorter in *palmarum,* longer in *parkeri*) and by no significant difference between northern and southern populations in the difference between inter-note interval and note duration (both significantly less than *palmarum*).

This species has the widest latitudinal geographic range and also the greatest variation in the duration of notes among individuals (Fig. 1C–I). Songs of northern individuals average lower-pitched than southern birds, with shorter notes: hoots from southeast Mexico to eastern Guatemala are 0.09–0.19 s long ($\bar{x}$ = 0.11 ± 0.02, N = 6 birds), with a mean dominant frequency of 1339 Hz, while hoots from Costa Rica to northwestern Ecuador are 0.12–0.23 s long ($\bar{x}$ = 0.17 ± 0.03, N = 7 birds), with mean 1428 Hz. Although the note duration of northern populations is significantly shorter than that of southern populations ($P < 0.001$), short and long notes occur in both populations (Fig. 1C–I). There also may be a tendency for northern birds to sing more notes, since we have heard no birds from Costa Rica to northwest Ecuador give more than 12 notes in a song; one recording from Colombia consists simply of six two-note songs which superficially suggest *G. minutissimum* (the notes, however, are much shorter [0.16–0.17 s] and the tempo different than that species). Geographic variation of this degree may be typical in a widespread small owl. For example, for *G. hardyi,* which also has a large geographic range, Vielliard (1989) noted variation in the number of notes (12–36) and in the tempo (10–13 notes/s) which appeared to correlate with distribution; and, for the European Little Owl (*Athene noctua*), Exo (1990) showed that British birds gave higher-pitched and longer calls than birds in Germany. Note also the geographic variation in *G. sanchezi* (above).

See above and under *G. palmarum* for a discussion of the song differences between it and *griseiceps.* The long series of relatively short notes with short inter-note intervals readily distinguish *griseiceps* from *G. sanchezi* and *G. minutissimum* (Table 1; Figs. 1–2). Note that populations of

griseiceps geographically nearest *sanchezi* have fast-paced, multiple-noted songs ($\bar{x}$ = 7 notes/song in Veracruz and Chiapas, Mexico) quite different from the higher pitched, slow-paced, one to three-note song of *G. sanchezi* (Fig. 1C vs Fig. 2A). Southern populations of *griseiceps* (eastern Panama/adjacent Colombia and northwestern Ecuador) have higher pitched and slower-paced songs in contrast to the lower pitched, faster-paced song of *parkeri* (Fig. 1G–I vs Fig. 3).

G. parkeri: songs comprise 2–4 relatively short, low-pitched hoots, and are characterized by a distinct, consistently increasing length of inter-note interval (Fig. 3; Table 1). Thus the second pause of a three-note song is significantly longer than the first (Table 1; $P < 0.01$), the effect to the human ear being that of slowing down or a hesitation before the last note of the song, e.g., "*hu hu, hu*". Although masked in Table 1, which combines all notes in songs to give a mean, the duration of notes also increases overall, with the last note of a song 0.01–0.10 s longer than the first ($\bar{x}$ = 0.04 s ± 0.02, N = 28 songs) ($P < 0.001$). Another distinctive feature of this species' song is the inter-song intervals are significantly shorter than in all other species in this complex (Table 1; $P < 0.05$).

The song of *parkeri* differs from *G. palmarum* and *G. griseiceps* by having fewer notes and from *G. sanchezi* and *G. minutissimum* in its short notes. It differs from all other taxa in this complex in tempo, in particular the increasing length of inter-note intervals, and in the very short inter-song interval.

G. minutissimum: the song of this species typically consists of two, low-pitched, long hoots separated by a pause about equal to the duration of the notes (Table 1; Fig. 2B). Three and four-noted songs have been recorded rarely (Sick 1993; D. Stotz, pers. comm.; B. Whitney, tape recording) and have long notes and pauses similar to two-note songs. The song of *minutissimum* is obviously different from that of all other species except *G. sanchezi* (Table 1; Figs. 1–3); distinctions between these two taxa are discussed under the latter.

Morphology.—When viewing specimens in series, three groups stand out immediately by virtue of their plumage coloration: the pale west Mexican birds (*G. palmarum*); the dark, reddish-brown birds from eastern Mexico to Brazil (*G. sanchezi, G. griseiceps, G. hardyi, G. minutissimum*); and the dark, gray-brown birds, with distinct white spots on their scapulars and wings, from the east slope of the Andes (*G. parkeri*). No sexual dimorphism in plumage is apparent in any of the taxa except *sanchezi,* in which females are redder than males.

Although birds from west Mexico have been labeled as three different subspecies (*palmarum, oberholseri,* and *griscomi*), when viewing series of all three in comparably fresh plumage, the only noticeable difference

is the more finely spotted, or flecked, head of specimens from southern Oaxaca, compared with birds from elsewhere in the range of *G. palmarum.* Binford (1989) also noted this character and suggested these birds may represent an undescribed subspecies. Moore (in Friedmann et al. 1950) questioned the validity of *oberholseri.* Our analysis supports Moore, and we propose that *oberholseri* be synonymized with *palmarum.* The subspecies *griscomi,* however, of the interior Río Balsas drainage, may be distinguishable from other west Mexican birds by its average greater size (Moore 1947), although larger series are desirable to evaluate fully the characters of this form.

Our sample, although larger than those used to describe the three subspecies of *G. griseiceps,* is insufficient to show significant mensural or plumage differences that correlate consistently with these subspecies. Although birds from Mexico through Honduras (*occultum* and *griseiceps*) average shorter-tailed than birds from Costa Rica and Panama (*rarum*), there is overlap in this character. Similarly, some birds from southeast Mexico have heavily spotted heads like birds from southern Central America. We propose that *G. griseiceps* can be considered monotypic until larger series of adult specimens in comparably fresh plumage are available to evaluate critically geographic variation.

On the whole, mensural differences are slight among the taxa in this complex. Although some differences are apparent, it is not clear what biological significance, if any, they may have. Male *G. palmarum* have significantly shorter wings than males of all other species ($P < 0.001$; Table 2) and have significantly longer tails than males of all other species except *G. sanchezi* (Table 2). The wing/tail ratio is least in the two northern species, *G. palmarum* and *G. sanchezi* (1.6) and greatest in *G. hardyi* and *G. parkeri* (1.9) of South America. Thus the two subtropical taxa (*sanchezi* and *parkeri*) are at opposite ends of this scale.

For the two species represented by adequate sample sizes for both males and females, *G. palmarum* and *G. sanchezi,* the sexes differ significantly in wing length, and *palmarum* females also have longer tails than males (Table 2; *t*-test, two-tailed, $P < 0.001$).

Plumage within the genus *Glaucidium* is, on the whole, remarkably uniform. For example, based solely on plumage coloration and pattern, *G. hardyi* was not recognized as a taxon separate from *minutissimum* until its distinctive voice was recorded. Nonetheless, the six species in the *G. minutissimum* complex show consistent plumage differences from one another and are illustrated in the Frontispiece which should be consulted for interpretation of colors used in the following descriptions. The number of tail bars noted below includes the distal bar which is near or at the tip

TABLE 2

MEAN (±SD) FOR SELECTED MEASUREMENTS (IN MM) OF THE *GLAUCIDIUM MINUTISSIMUM* COMPLEX

	Wing (chord)		Tail (central rectrix)		Mass
	Male	Female	Male	Female	Males only
G. palmarum[a]	82.9 (±1.9) N = 79	85.9 (±1.8) N = 17)	52.5 (±1.6) N = 74	54.5 (±1.2) N = 16	44.9 (±2.5) N = 19
G. sanchezi	87.3 (±1.4) N = 6	91.0 (±2.4) N = 5	52.7 (±2.8) N = 5	55.0 (±0.5) N = 4	53.5 (±2.1) N = 2
G. griseiceps[b]	87.2 (±2.7) N = 10		47.8 (±1.8) N = 10		50.6 (±1.1) N = 3
G. parkeri	93.2 (±3.9) N = 3		50.0 (±3.4) N = 3		61.6 (±2.5) N = 3
G. hardyi	92.2 (±1.6) N = 7		46.8 (±1.8) N = 7		55.1 (±3.3) N = 4
G. minutissimum	86.4 (±3.9) N = 6		49.7 (±4.2) N = 6		

[a] Includes *oberholseri* and *griscomi.*
[b] Includes *occultum* and *rarum.*

of the rectrices and can be absent if the tail tip is extremely worn. In life, the basal 1–2 tail bars are covered by the crissum and uppertail coverts.

G. palmarum: crown and nape grayish tawny-brown, with extensive whitish to pale buff spotting, and slightly grayer than tawny olive-brown back. Bars on the closed wings are formed by pale cinnamon to buffy-white spots on the outer webs of the primaries and secondaries. Tail with six or seven white to buffy-white bars. Sides of chest and streaking on underparts cinnamon-brown to dark cinnamon-brown.

Palmarum is paler overall than *G. sanchezi,* its head being less contrastingly gray than male and less rich brown than female *sanchezi* with, on average, more extensive pale head spots; the chest sides and underpart streaks are paler, cinnamon-brown. From *G. griseiceps* and *G. minutissimum, palmarum* differs in the same respects as it does from *sanchezi,* except that the extent of pale head spotting is similar in all three and the tail of *palmarum* has six or seven pale bars. From *G. hardyi, palmarum* differs in its overall paler plumage, less contrasting gray head, and in six or seven pale tail bars. From *G. parkeri, palmarum* is told by its paler coloration, lack of bold white spots on the scapulars and wings, and in six or seven pale tail bars.

G. sanchezi: this species is unique in the Least Pygmy-Owl complex in that the sexes are dichromatic. The male has a gray-brown crown and

nape with fine pale buff to whitish spots on the forecrown; the nape contrasts slightly with the grayish olive-brown back. Bars on the closed wings are formed by pale cinnamon to pale buff spots on the outer webs of the primaries and secondaries. The chest sides and underpart streaks are dark olivaceous tawny-brown, and the tail has six whitish bars. The female has the crown, nape, and upperparts washed with cinnamon and dorsally is overall fairly uniform and distinctly redder than the male. The forecrown is finely spotted with pale buffy-cinnamon. The chest sides and underpart streaks are dark rufous-brown, and the six pale tail bars are tinged buff to pale cinnamon. In two of six males and one of four females the pale head spots extend back laterally to the nape.

Male *sanchezi* differ from *G. griseiceps* and *G. minutissimum* by their more olivaceous, less rufous upperparts and underpart streaks and from *minutissimum* by their grayer head. Female *sanchezi* differ from *griseiceps* by the cinnamon-brown cast to their head. Both sexes of *sanchezi* also differ from *griseiceps* and *minutissimum* in their six pale tail bars and, on average, less extensive pale spotting on the head. From *G. hardyi, sanchezi* differs in its six pale tail bars, less contrasting gray head, slightly paler and more olivaceous upperparts, and, on average, less extensive pale crown spotting. Some *hardyi* and male *sanchezi,* however, are extremely similar in overall coloration. From *G. parkeri, sanchezi* differs in its six pale tail bars and paler and redder plumage that lacks bold white spots on the scapulars and wings. See under *G. palmarum* for differences between it and *sanchezi.*

G. griseiceps: crown, nape, and upperparts rich olivaceous-brown to rufous-brown with a grayer wash to the head and whitish to buffy-white spotting on the crown and nape. Bars on the closed wings are formed by pale cinnamon spots on the outer webs of the primaries and secondaries. Tail with five white to buffy-white bars. Chest sides and underpart streaks rufous-brown.

From *G. minutissimum, griseiceps* differs in its grayer head, darker and redder chest and underpart streaking but less rufescent back. From *G. hardyi, griseiceps* differs in its less contrasting gray head, and redder upperparts and chest and underpart streaking. From *G. parkeri, griseiceps* differs in its paler and redder plumage that lacks bold white spots on the scapulars and wings. See under *G. palmarum* and *G. sanchezi* for differences between those species and *griseiceps.*

G. minutissimum: crown and nape dusky cinnamon-brown with whitish to buffy-white spots extending back to the nape; back rufous-brown. Bars on the closed wings are formed by pale cinnamon spots on the outer webs of the primaries and secondaries. Tail with five white to buffy-white bars. Chest sides and underpart streaks rufous-brown to dark cinnamon-brown.

From *G. hardyi, minutissimum* differs in its redder crown, upperparts, chest sides, and underpart streaks. From *G. parkeri, minutissimum* differs in paler and redder plumage that lacks bold white spots on the scapulars and wings. See under *G. palmarum, G. sanchezi,* and *G. griseiceps* for differences between those species and *minutissimum.*

G. hardyi: crown and nape brownish-gray with extensive white spotting, contrasting slightly with dark gray-brown back. Bars on the closed wings are formed by pale cinnamon spots on the outer webs of the primaries and secondaries. The tail has five whitish bars. The chest sides and underpart streaks are dusky cinnamon-brown to brown. From *G. parkeri, hardyi* differs in its redder plumage that lacks bold white spots on the scapulars and wings. See other taxa for differences between them and *hardyi.*

G. parkeri: a distinctive species characterized by its dark gray-brown to brown crown, nape, and upperparts with extensive whitish head spotting, bold white spots on the scapulars, and contrasting white spots and bars on the wings; its tail has five white bars (Robbins and Howell 1995). See other taxa for differences between them and *parkeri.*

Distribution and habitat.—The six species in the *G. minutissimum* complex have allopatric distributions (see Frontispiece). With the exception of *palmarum,* all Least Pygmy-Owls inhabit the upperstory of tall, humid forest, helping explain why they are often overlooked and why so few specimens exist of the Central and South American species.

G. palmarum: endemic to western Mexico where it occupies a range of habitats, in arid to semihumid conditions, from near sea level to 1500 m elevation (Buchanan 1964, Howell, pers. obs.). It occurs on the Pacific Slope from central Sonora (foothills east of Hermosillo; Howell and S. Webb, pers. obs.) to central Oaxaca (foothills inland of Puerto Angel; Howell and P. Pyle, pers. obs.) and also in the Balsas drainage of southern Morelos (Friedmann et al. 1950, Fig. 1B) and northern Guerrero (Friedmann et al. 1950). There is no indication that the ranges of *G. palmarum* and *G. griseiceps* approach one another in the Isthmus of Tehuantepec since they occupy different habitats (arid thorn forest vs humid rain forest); their allopatric ranges are typical of numerous Pacific and Atlantic slope forms in this region, e.g., *Chlorostilbon auriceps, Tityra semifasciata griseiceps,* and *Cyanocompsa parellina indigotica* on the Pacific slope vs *C. canivetii, T. s. personata,* and *C. p. parellina* on the Atlantic slope (Miller et al. 1957, Binford 1989, Howell 1993).

In much of its range, *palmarum* occurs in tropical deciduous forest (thorn forest), usually in foothills, whereas *G. brasilianum* is common in lowlands. These two species do occur sympatrically, however, and their exact ecological differences have yet to be determined. *Palmarum* occurs

from thorn forest through semideciduous forest up into dry oak woodland and, less often, dry pine-oak woodland where it can occur sympatrically with the highland species *G. gnoma* (Schaldach 1963). In much of western Mexico, *palmarum* is, at least locally, fairly common to common (considered "very common" by Binford [1989]). In southern Nayarit and Colima, the highest density of *palmarum* occurs in barrancas at the upper edge of the tropical deciduous forest (Schaldach 1963, Howell, pers. obs.). It also has been noted from "palm forest on a low ridge near the sea" (Nelson 1901) and from "swamp forests" (Binford 1989).

G. sanchezi: endemic to northeastern Mexico where it occurs locally in southern Tamaulipas and eastern San Luis Potosí. It inhabits subtropical, humid evergreen and semideciduous forest from 900 to 2100 m elevation (Lowery and Newman 1949, Webster 1974, J. Arvin, pers. comm., Howell, pers. obs.). Unlike *palmarum* in western Mexico, *sanchezi* appears to be locally fairly common to uncommon (Arvin, pers. comm., Howell, pers. obs.).

G. griseiceps: occurs from northern Oaxaca (Binford 1989; Howell, tape recording) and southeastern Veracruz (Fig. 1C) south on the Atlantic Slope of Mexico and Central America to northwestern Colombia (A.O.U. 1983, Sibley and Monroe 1990). There also is one record from 1300 m elevation on the Pacific Slope of Guatemala (B. Whitney, tape recording). The first records of this species south of the Panamanian/Colombian border (Hilty and Brown 1986) were of two pairs seen and recorded (LNS 63147, 63168, 63174, 63424–5; Fig. 1H–I) in mid-July 1990, north–northwest of Alto Tambo, Prov. Esmeraldas, Ecuador (00°57′N, 78°33′W), by Robbins during the course of ANSP inventory work. Even after voice playback, both pairs remained over 35 m up in the subcanopy of pristine, wet evergreen hill forest at ca 350 m elevation. *Griseiceps* inhabits tropical humid evergreen forest (rain forest) and forest edge from near sea level to 1300 m elevation. It is uncommon to locally fairly common (Stiles and Skutch 1989, Howell, pers. obs.) and has been considered "rare to locally uncommon" (Ridgely and Gwynne 1989).

G. parkeri: known from 1450–1975 m elevation on outlying ridges of the east slope of the Andes of Ecuador and Peru, and it may well occur also in southeastern Colombia (Robbins and Howell 1995). It occurs in subtropical evergreen forest and, while apparently not particularly uncommon, like other humid forest forms of the Least Pygmy-Owl complex, it may be overlooked easily.

G. hardyi: this species is generally considered uncommon and inhabits the upperstory of humid evergreen forest (rain forest), specifically tall terra firma, transitional, and varzea forest, over much of Amazonian South America, being unknown above 350 m elevation (Vielliard 1989, Parker

1982, Parker and Remsen 1987). It is unrecorded from Colombia, Ecuador, and north of the Río Amazonas and west of the Río Ucayali drainage in Peru. In addition to the records listed by Vielliard (1989), König (1991), and specimen localities listed by Robbins and Howell (1995), T. Parker (pers. comm.) recorded this species as far north and west in Peru as the right (east) bank of the Río Ucayali, southeast of Pucallpa, Depto. Ucayali. *G. hardyi* is further known from several localities in southeastern Peru (Parker 1982, pers. comm.) and northern Bolivia (Parker and Remsen 1987, Remsen and Traylor 1989). Parker (pers. comm.) also found the species in Brazil on the west bank of the Río Tapajós at Itaitus, Pará, and south of Alta Floresta, Río Teles Pires, Mato Grosso. The specimen record by M. Cohn-Haft (pers. comm.) at ca 80 km north of Manaus, Amazonas, Brazil, is the westernmost site this species has been found north of the Río Amazonas.

G. minutissimum: with the realization that the Amazonian lowlands are occupied by *G. hardyi,* the range of true *minutissimum* appears to be restricted to southeastern Brazil and adjacent Paraguay (Vielliard 1989). This species occurs in tropical humid evergreen forest (rain forest) and edge from sea level to 1000 m elevation and seems intolerant of secondary forests (D. Stotz, pers. comm.). It is uncommon to locally fairly common, and in southeast Brazil it appears commonest at foothill elevations of 500–800 m (Stotz, pers. comm.).

Conclusions.—The differences in song among members of the *G. minutissimum* complex are comparable to or greater than other species-level song differences within genera of small owls such as *Glaucidium* (e.g., *G. brasilianum* and *G. palmarum*), *Otus* (e.g., *O. kennicottii, O. seductus,* and *O. cooperi*; A.O.U. 1983, Hardy et al. 1990), and *Aegolius* (e.g., *A. acadicus* and *A. ridgwayi*; A.O.U. 1983, Hardy et al. 1990). Further, no song types of any one species in the *minutissimum* complex have been heard in populations of the other five species. These vocal dissimilarities are supported by differences in structure, plumage, and habitat. In addition, the six species of the *minutissimum* complex are allopatric. Criteria for both biological and phylogenetic species concepts appear to be met, and thus we propose the following revision. Suggested English names reflect the distributions of the four forms that we have elevated to species rank.

Glaucidium palmarum Colima Pygmy-Owl

Glaucidium palmarum Nelson 1901, Auk 18, p. 46.

Type specimen.—USNM No. 155955, adult female. Collected 5 April 1897 by E. W. Nelson and E. A. Goldman.

Type locality.—Arroyo de Juan Sanchez, Territory of Tepic, Mexico.

Measurements of type.—Wing 87 mm; tail 56 mm.

Geographic range.—Endemic to western Mexico from Sonora to Oaxaca (sea level–1500 m).

Characters.—Relatively long-tailed and short-winged. Plumage distinctive: relatively pale, grayish tawny-brown overall, with 6–7 pale tail bars. Song: 2–24 short notes separated by long pauses, the longest pause between the first and second notes.

Specimens examined.—102 skins, six tape recordings (listed by Robbins and Howell 1995).

Glaucidium sanchezi Tamaulipas Pygmy-Owl

Glaucidium minutissimum sanchezi Lowery and Newman 1949, Occas. Papers LSUMZ, 22, pp. 1–4.

Type specimen. LSUMZ No. 11002, adult male. Collected 14 May 1947 by R. J. Newman.

Type locality.—Llano de Garzas, near Cerro Coneja, San Luis Potosí, Mexico.

Measurements of type.—Wing 90.1 mm; tail 57 mm.

Geographic range.—Endemic to NE Mexico in SW Tamaulipas and E San Luis Potosí (900–2100 m).

Characters.—Relatively long-tailed. From *G. palmarum* by darker plumage (cinnamon-brown overall). From other forms by six pale tail bars and reduced and finer pale flecks on crown. Sexes dimorphic (female redder). Song: 1–3 high-pitched, long notes separated by long pauses.

Specimens examined.—13 skins, nine tape recordings (listed by Robbins and Howell 1995).

Glaucidium griseiceps Central American Pygmy-Owl

Glaucidium griseiceps Sharpe 1875, Ibis 1875, p. 41.

Type specimen.—Lectotype: British Museum No. 75.6.14.45, "Ex. coll. Bouvier", unsexed, undated.

Type locality.—Veragua (Panama) and Chisec and Choctum (Guatemala); restricted to tropical lowlands (Coban) of Alta Vera Paz, Guatemala, by Griscom (1931).

Measurements of type.—Wing 87 mm; tail 52 mm.

Geographic range.—SE Mexico to NW South America (sea level–1300 m).

Characters.—Relatively short-tailed. Plumage relatively dark, rufous-brown overall with five pale tail bars. Plumage redder overall than *G.*

parkeri or *G. hardyi,* crown grayer than *G. minutissimum.* Song: 2–18 steadily paced notes of approximately equal duration.

Specimens examined.—13 skins, 14 tape recordings (listed by Robbins and Howell 1995).

Glaucidium parkeri Subtropical Pygmy-Owl

Glaucidium parkeri Robbins and Howell 1995, Wilson Bull. 107, pp. 1–6.

Type specimen. ANSP No. 185160, adult male. Collected 22 July 1992 by F. Sornoza M.

Type locality.—Ecuador: Prov. Zamora-Chinchipe; Panguri, ca 12 km NE San Francisco del Vergel, 04°37′S, 78°58′W.

Measurements of type.—Wing 91.8 mm; tail 48.5 mm.

Geographic range.—E slope of Andes in Ecuador and Peru (1450–1975 m).

Characters.—Relatively long-winged. Plumage distinctive: relatively dark gray-brown overall with bold white spots on crown, nape, and wing coverts; five pale tail bars. Song: two–four notes with increasing length of pause between notes; short inter-song interval.

Specimens examined.—three skins, four tape recordings (listed by Robbins and Howell 1995).

Glaucidium hardyi Amazonian Pygmy-Owl

Glaucidium hardyi Vielliard 1989, Revta. Bras. Zool., 6, pp. 685–693.

Type specimen.—ZUEC (Universidade Estadual de Campinas, Brazil) No. 1194, male. Collected 16 April 1983 by J. Vielliard.

Type locality.—20 km SW Presidente Medici Rondônia, Brazil.

Measurements of type.—Wing 94 mm; tail 52 mm.

Geographic range.—Amazonian South America (sea level–350 m).

Characters.—Relatively long-winged. Plumage relatively dark, grayish rufous-brown with five pale tail bars. Head and upperparts grayer than *G. griseiceps* and *G. minutissimum.* Song: 12–36 notes given in rapid trill.

Specimens examined.—seven (listed by Robbins and Howell 1995).

Glaucidium minutissimum Brazilian Pygmy-Owl

Strix pumila Temminck 1821, Pl. col., livr. 7, pl. 39.
Strix minutissima (Wied) 1830, Beitr. Naturg. Bras., 3, pt. 1, p. 242.

Type specimen.—Syntypes: AMNH No. 6345 (male), 6345 bis (female), undated.

Type locality.—Interior state of Bahia, Brazil.

Measurements of syntypes.—Wing 87.7, 90.8 mm; tail 50.3, 50.6 mm.

Geographic range.—SE Brazil and adjacent Paraguay.

Characters.—Relatively short-winged. Plumage relatively dark, rufous-brown overall with five pale tail bars. Crown redder than *G. griseiceps* or *G. hardyi.* Song: two–four long notes separated by shorter pauses than *G. sanchezi.*

Specimens examined.—13 skins, five tape recordings (listed by Robbins and Howell 1995).

ACKNOWLEDGMENTS

We are indebted to a number of first-rate field observers who have shared with us their tape recordings of the *G. minutissimum* complex: John C. Arvin, Robert A. Behrstock, Ben B. and Lula C. Coffey, Paul Coopmans, Jeff Kingery, Greg W. Lasley, Francisco Sornoza M., F. Gary Stiles, Bret Whitney, and David E. Wolf. Luis F. Baptista kindly made available his sound analysis laboratory at the California Academy of Sciences and offered helpful comments on spectrogram interpretation. Nigel J. Collar and Peter Colston (British Museum) kindly provided data on the type series of *G. griseiceps.* Rafael G. Campos R. and Douglas F. Stotz and Mario Cohn-Haft provided data from Costa Rican and Brazilian pygmy-owls, respectively. Arvin, Stotz, and the late Theodore A. Parker, III, contributed ecological and distributional data on *G. sanchezi, G. minutissimum,* and *G. hardyi,* respectively. We are indebted to Sophie Webb for painting the color frontispiece. The following museums and persons gave permission to borrow and examine specimens in their care: American Museum of Natural History (Mary LeCroy), Bell Museum of Natural History, Univ. of Minnesota (Gary A. Voelker), Carnegie Museum of Natural History (Kenneth C. Parkes), Delaware Museum of Natural History (Gene Hess), Field Museum of Natural History (Scott M. Lanyon and David E. Willard), Louisiana State University Museum of Natural Science (J. Van Remsen and Steve W. Cardiff), Moore Laboratory of Zoology, Occidental College (John C. Hafner), Museum of Comparative Zoology, Harvard University (MCZ; Raymond A. Paynter), National Museum of Natural History, Smithsonian Institution (USNM; Gary R. Graves), and Western Foundation of Vertebrate Zoology (Lloyd F. Kiff). Ned K. Johnson, Richard Prum, Sophie Webb, and an anonymous referee made helpful comments on the manuscript. Peter Pyle helped significantly with statistical analysis. This is contribution number 606 of Point Reyes Bird Observatory.

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Wilson Bull., 107(1), 1995, pp. 26–39

HABITAT SELECTION IN WOODLAND NEARCTIC–NEOTROPIC MIGRANTS ON THE ISTHMUS OF TEHUANTEPEC I. AUTUMN MIGRATION

KEVIN WINKER[1,2]

ABSTRACT.—The distribution of autumn migrants among Neotropical wooded habitats was examined using mist nets in a rainforest region of southern México. Capture distributions and local movements from north and south (as reflected by net captures) were examined in 17 species. All species showed significant nonrandom distributions. Captures from the north were not more frequent than expected by chance. Local diurnal movements, therefore, do not reflect the known latitudinal movements occurring in these species, which makes it unlikely that local habitat use is simply the result of directional wandering. Although 65% of captured individuals were first-year birds having no previous experience with tropical rainforest, capture distributions suggested species-specific selectivity to a rather high degree. Also, in the 10 species with adequate sample sizes, distributions between early- and later-day captures tended to be remarkably constant. Habitat selection in these species may be largely endogenous. *Received 30 Nov. 1993, accepted 25 Sept. 1994.*

Habitat selection in birds has long been an important area of study (see Hildén 1965, Cody 1985). The postbreeding, pre-wintering movements of migrant species brings a different aspect to this field, however. The high degree of transience found at this time can result in the co-occurrence of species which overlap neither in breeding nor in wintering ranges in habitats that are unsuitable for either. Further, although small migrants probably need to deposit fat for migration at sites between their breeding and wintering ranges (see Nisbet et al. 1963, Berthold 1975, Bairlein 1987, Winker et al. 1992a), their ability to store energy and their sheer mobility suggest that they may not depend upon food resources in all of the habitats where they occur during migration.

Questions regarding community structure, coexistence, and niche breadth thus take on new dimensions at migratory stopover sites. Habitat selection and use, key components of these questions, have hardly begun to be examined in migration (see Parnell 1969; Berthold et al. 1976; Bairlein 1981, 1983; Hutto 1985a; Berthold 1989; Moore et al. 1990; Winker et al. 1992a, b). They have not been examined at stopover sites in the Neotropics.

This study addresses basic questions of habitat selection among migrants at a Neotropical site in southern México. Are wooded habitats used indiscriminately as they are encountered by migrants or does selection

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occur? What is the nature of selection, if it occurs? Do migrants sample the available macrohabitats, then gradually settle in suitable areas? The area chosen to study these questions, the Isthmus of Tehuantepec, is the northernmost narrowing of the North American continental landmass. This region theoretically causes a funneling and concentration of Nearctic–Neotropic landbird migrants, making it likely that stopover sites are heavily used. It also contains the northernmost Neotropical rainforest (Pennington and Sarukhán 1968). Thus, first-year autumn migrants on the Isthmus have no previous exposure to woodlands of this type. Examining the diurnal distributions of these nocturnal migrants under such conditions can give insight into whether habitat selection is, in part, an endogenous phenomenon (e.g., Bairlein 1981, 1983; Berthold 1989).

STUDY SITE AND METHODS

The study site is located just south of the Estación de Biología Tropical "Los Tuxtlas" of the Instituto de Biología of the Universidad Nacional Autónoma de México (UNAM), in the Sierra de los Tuxtlas, southern Veracruz, México (18°34′30″N, 95°04′20″W). This area occupies the NW region of the Isthmus of Tehuantepec. The site is located near the coast of the Gulf of México. It is 5 km S and 3 km W of the coastline, which in this area runs approximately NNW–SSE.

Thirty-six standard nylon mist nets (12 × 2.6 m) were placed 30 m apart in an area offering mature and second growth wooded habitats. Nets were oriented in an E–W direction. This orientation was chosen to enable the detection of diurnal movement inland from the coast (i.e., from the NE), or along the axis of normal diurnal migration in this area (from the NW–N). It is assumed that the side upon which the bird entered the net indicates (on a gross scale) the direction of local movement before capture. The site was composed of primary forest (selva) bordered by second growth woodland (acahual), which in turn changed gradually into old pasture (not sampled). Nets were set in the woodlands, with half in primary forest and half in second growth. These woodlands were not homogeneous, however, and analyses presented consider both the macro- and microhabitat scales. Nets were opened whenever weather permitted during daylight hours, and 12,608 net-h were accumulated between 5 September and 15 November 1992. Sample effort was equal among all nets. When removing birds from nets, the time, net, and side of capture (N or S) were recorded for every individual.

Vegetation analysis was conducted at each net site, following the methods of James and Shugart (1970) with the slight modifications outlined by Winker et al. (1992b). However, the analysis was structural only—species composition was not considered (see Appendix I).

Shortfalls of the methodology.—In a study like this, mist nets sample a non-uniform, three-dimensional space in a relatively uniform manner. In low second growth, the vertical vegetative stratum is fully sampled, while in tall primary forest, nets sample only a small part of this stratum. Species are adequately sampled when their activities are typically in the understory or near the ground. Species whose activities occur in and near the canopy will probably show a biased capture distribution, with relatively more captures occurring in low-stature vegetation. Thus, captures in some species may not reflect that species' macrohabitat distribution. For these reasons, I do not discuss optimal or preferred habitats, believing that such determinations require additional data.

There is a positive aspect to this problem, however. Obtaining a relatively uniform, largely

two-dimensional sample of a three-dimensional environment, without collapsing these three dimensions into two, gives better resolution when comparing spatial distributions among species. For example, in the sampling scheme used in this study, netting data can detect a difference between the distributions of a canopy and ground-level species that might not be apparent with an approach (e.g., censusing) that collapses the third dimension. Of course, our understanding of bird distributions among habitats would be much improved if we could acquire two-dimensional samples from higher levels in the third dimension.

Data analysis.—To examine characteristics of capture distributions, abundance differences among species were eliminated by standardizing the captures at each net to represent the percentage of total captures of each species. Recaptures were ignored. Some explanation of the statistical methods used are in order: *G-test with Williams' correction.* When used with unstandardized side-of-capture data, this test examines whether more captures occurred due to local N–S or S–N movement than would be expected by chance. It is also used to compare early and later-day capture distributions between macrohabitat types. *Cluster analysis (UPGMA method).* This test is used to depict graphically similarities among net locations according to the structure of the surrounding vegetation (Fig. 1, Appendix) and among species' capture distributions (Fig. 2). Clustering nets on the basis of vegetation structure (see Fig. 1) revealed three groups: primary forest, second growth, and a single outlier. Because the outlier was in primary forest, it is included in this group for macrohabitat comparisons. *Kolmogorov-Smirnov test for "uniform" distribution.* This tests whether the distribution of captures might have come from a population uniformly distributed among capture points. Capture distribution is compared against random numbers taken from a distribution of values uniformly distributed between zero and the maximum percentage of total captures occurring among the nets for a particular species. Significant departure from random "uniformity" (when sample effort is uniform) suggests nonrandom distribution. *Kolmogorov-Smirnov 2-sample test, comparing capture distributions between species pairs.* This test compares the shapes of the distributions of standardized captures among the habitat array. It answers the question of whether distributions differ between species pairs. *Sign test.* As long as one uses standardized data, this test examines a different aspect of the question of how species are similar or dissimilar in their capture distributions. In this case, it essentially tests for differences between species in the breadth of occurrence among the 36 possible capture points. For example, species very dissimilar in two-dimensional distribution (e.g., one occurs largely in primary forest, the other in second growth) may be similar in the specificity or generality of their distributions. As will be seen, differences in distribution must be rather strong to be significant, using this test. Differences were significant when one of the two species occurred with a greater or lesser relative frequency (percentage of total captures) at about 70–80% of the total number of nets at which both species occurred. For example, a comparison of species *a* and *b* would show a significant difference if species *a* occurred with greater relative frequency at 75% of the total nets at which both species occurred.

RESULTS

Seventeen species were chosen for analysis based on their capture frequencies (see Table 1; $N = 1442$ individuals). The percentage of captures occurring from birds entering nets from the north ranged from 44.1% (Worm-eating Warbler, WEWA) to 72.4% (Swainson's Thrush, SWTH; Table 1), averaging 53.3% over all of the captures of these species (all scientific names are in Table 1). Despite the high percentage of captures

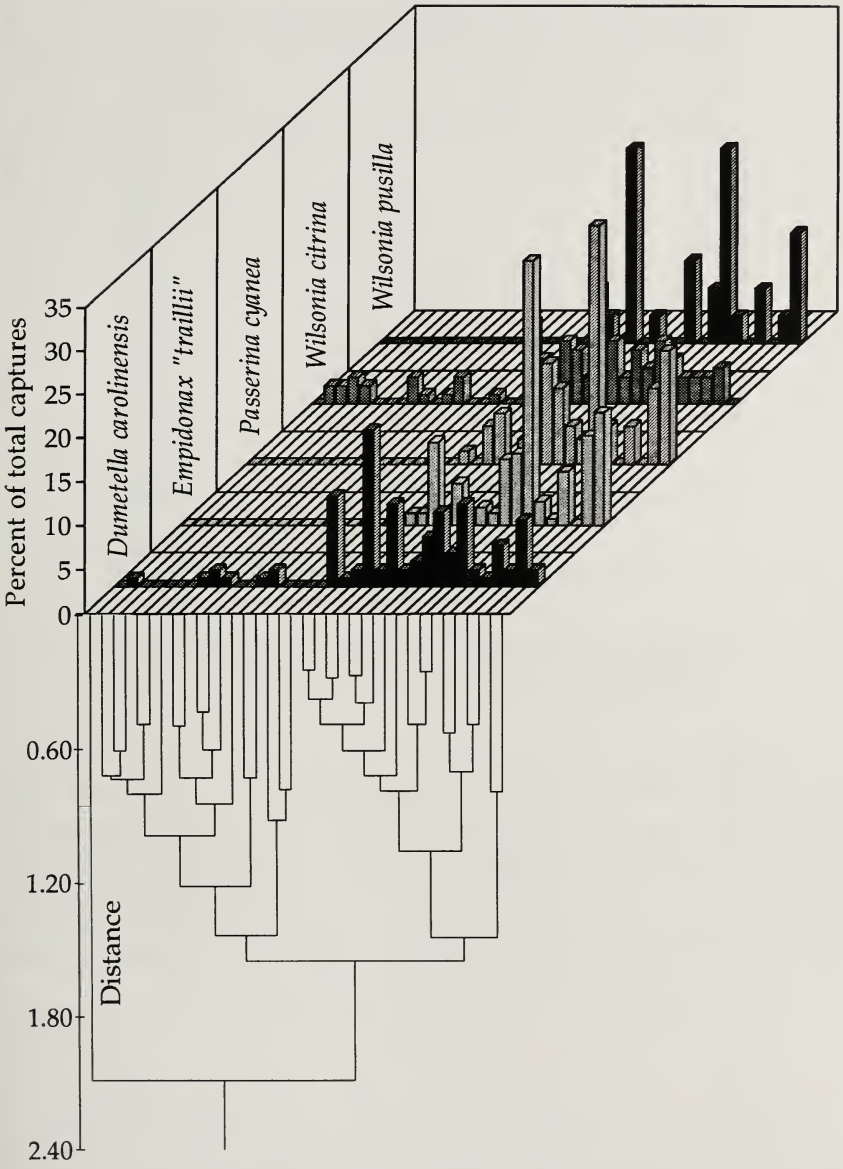

FIG. 1. Relationships among the 36 net locations in vegetation structure (dendrogram) and the capture distributions among these nets of five species that are well sampled using mist nets. The rightmost cluster of 18 locations is second growth; the remainder are primary forest.

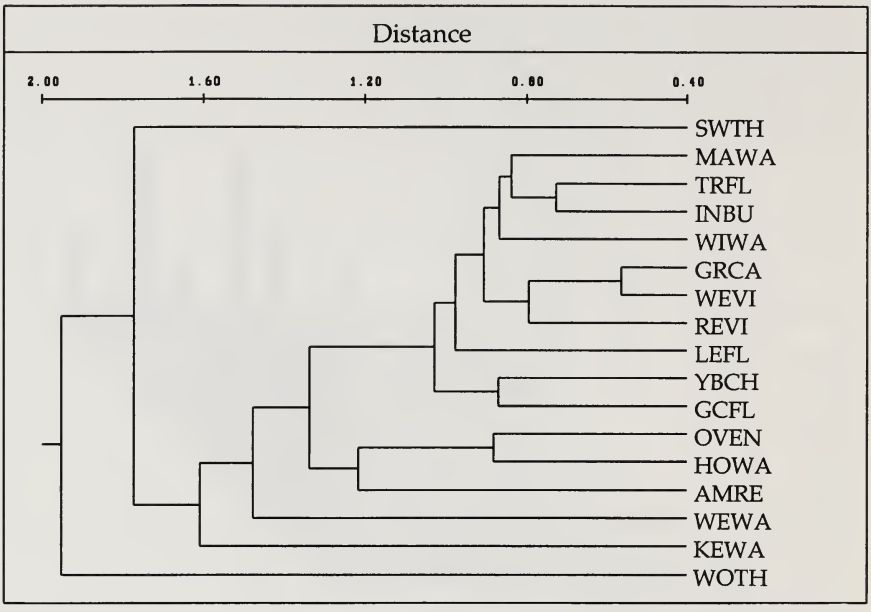

FIG. 2. Dendrogram of similarities in capture distributions among 17 migrant species (UPGMA clustering method). Name codes are in Table 1.

from the north in Swainson's Thrush (clearly an outlier; see Table 1), movements (as reflected in side-of-capture data) were not significantly different from random in any species (Table 1). The local, diurnal movements of the captured individuals, therefore, do not reflect the directional movements that we know are occurring on a seasonal, latitudinal scale. This realization has important consequences from the perspective of habitat selection: The vast majority of captured individuals are not occurring in the available habitats as a result of directional wandering.

If local captures do not reflect the seasonal direction of movement, there is a greater possibility that an individual's presence in a particular habitat is due to factors other than the simple fact that the habitat patch lies between the individual and its destination. Are such factors operating? This can be answered by determining whether individuals are distributed randomly among the available habitats. All of the 17 species examined showed highly significant nonrandom capture distributions (Table 1; Kolmogorov-Smirnov test against a random "uniform" distribution; $P < 0.001$). Habitat selection, therefore, seems to occur in all of the species examined.

If migrants were sampling available macrohabitats, then gradually set-

TABLE 1

SAMPLE SIZES OF COMMON MIGRANTS AND CAPTURE PERCENTAGES OCCURRING ON THE NORTH SIDE OF THE NETS, WITH RESULTS OF STATISTICAL TESTS EXAMINING DIRECTIONALITY (*G*-TEST) AND CAPTURE DISTRIBUTIONS[a]

Common name	Scientific name	Namecode	N	%	$G_{adj.}$[b]	P[b]	Z[c]	P[c]
Great Crested Flycatcher	*Myiarchus crinitus*	GCFL	46	56.5	0.39	$0.9 > P > 0.5$	4.00	0.000
"Traill's" Flycatcher	*Empidonax "traillii"*	TRFL	148	55.4	0.86	$0.5 > P > 0.1$	4.13	0.000
Least Flycatcher	*E. minimus*	LEFL	32	56.3	0.25	$0.9 > P > 0.5$	3.98	0.000
Gray Catbird	*Dumetella carolinensis*	GRCA	107	49.5	0.00	$1.0 > P > 0.9$	3.77	0.000
Wood Thrush	*Hylocichla mustelina*	WOTH	60	58.3	0.83	$0.5 > P > 0.1$	2.13	0.000
Swainson's Thrush	*Catharus ustulatus*	SWTH	29	72.4	3.02	$0.1 > P > 0.05$	2.82	0.000
White-eyed Vireo	*Vireo griseus*	WEVI	140	53.6	0.36	$0.9 > P > 0.5$	3.64	0.000
Red-eyed Vireo	*V. olivaceus*	REVI	273	48.0	0.22	$0.9 > P > 0.5$	3.54	0.000
Magnolia Warbler	*Dendroica magnolia*	MAWA	83	54.2	0.29	$0.9 > P > 0.5$	3.57	0.000
American Redstart	*Setophaga ruticilla*	AMRE	51	54.9	0.24	$0.9 > P > 0.5$	3.00	0.000
Worm-eating Warbler	*Helmitheros vermivorus*	WEWA	34	44.1	0.23	$0.9 > P > 0.5$	3.47	0.000
Ovenbird	*Seiurus aurocapillus*	OVEN	110	60.0	2.21	$0.5 > P > 0.1$	2.24	0.000
Kentucky Warbler	*Oporornis formosus*	KEWA	87	52.9	0.14	$0.9 > P > 0.5$	2.50	0.000
Hooded Warbler	*Wilsonia citrina*	HOWA	97	52.6	0.13	$0.9 > P > 0.5$	2.34	0.000
Wilson's Warbler	*W. pusilla*	WIWA	31	45.2	0.14	$0.9 > P > 0.5$	4.17	0.000
Yellow-breasted Chat	*Icteria virens*	YBCH	45	46.7	0.10	$0.9 > P > 0.5$	4.00	0.000
Indigo Bunting	*Passerina cyanea*	INBU	69	59.4	1.22	$0.5 > P > 0.1$	4.05	0.000

[a] Captures from the north were no higher than expected by chance. In contrast, capture distributions are all significantly different from random "uniform" distributions.
[b] *G*-test with Williams' correction: associated *G*- and *P*-values; see Sokal and Rohlf (1981).
[c] Kolmogorov-Smirnov goodness of fit test against the uniform distribution: associated *Z*- and *P*-values.

tling in suitable patches, there should be differences between early- and later-day macrohabitat distribution patterns. Sample sizes were not suitable for this analysis in all species. Among the 10 species with ≥60 individuals captured, none showed differences between early- (<10:01 h) and later-day (>10:01 h) capture distributions in primary forest and second growth (*G*-test with Williams' correction; $G_{adj} > 0.10$). Thus, patterns of capture at the macrohabitat level do not seem to change during the day.

At the microhabitat level, changes in distribution during the day might be expected under some conditions. Less-preferred areas, or areas that were not harvested in the morning, may be preferred later in the day. Also, diurnal changes in prey availability, or prey-switching, could cause microhabitat shifts. I have observational data (unpubl.) suggesting both of these may occur among migrants foraging at a stopover site in Minnesota (autumn 1987), but to my knowledge these spatial shifts have not been documented quantitatively in woodland birds (although they occur in wintering shorebirds; see Connors et al. 1981). Analysis of distributions on a microhabitat scale (net-by-net) between early- (<10:01) and later-day (>10:01) captures revealed a significant change in only one species of the ten in which 60 or more individuals were captured. The Kentucky Warbler (KEWA) showed a significant shift in capture distributions between early- and later-day captures (Kolmogorov-Smirnov two-sample test; $P = 0.037$). The other nine species examined were remarkably constant in their distributions between these periods (same test; $P > 0.5$).

It is apparent that distributions can differ markedly among species (Fig. 1). While species may theoretically exist in relative separation in multidimensional niche space, it is highly unlikely that an array of 36 mist nets sampling two physical dimensions can detect much of this separation, even if it exists. Despite this unlikelihood, of the 136 possible between-species comparisons, fully 40 (29.4%) showed significant differences in distribution (Table 2). This seems a rather high degree of species-level differentiation in how individuals are distributed within the available habitat array.

A cluster dendrogram of similarities in distributions among species (Fig. 2) reveals groupings that might have been roughly predicted, given an understanding of these species in the field. The natural cluster of species from Magnolia Warbler (MAWA) to Great Crested Flycatcher (GCFL) constitutes a group whose captures occurred primarily (and in some cases exclusively) in second growth woodland. The grouping of the Magnolia Warbler with "Traill's" Flycatcher (TRFL) and the Indigo Bunting (INBU) is probably inaccurate with respect to macrohabitat use. While this grouping accurately reflects distributions in sampled space,

Magnolia Warblers (unlike "Traill's" Flycatchers and Indigo Buntings) regularly occur in primary rainforest; their activity levels in this habitat tend to be nearer the canopy than at net levels, however (pers. obs.). The foraging levels of White-eyed (WEVI) and Red-eyed vireos (REVI), Wilson's (WIWA) and Worm-eating warblers (WEWA), and the American Redstart (AMRE) also tend to be higher in primary forest, making their exact position in Fig. 2 from the macrohabitat perspective unclear. Although Fig. 2 is useful for a broad-brush view of interspecific distributional relationships, Table 2 more accurately depicts real differences.

Another question of habitat selection is whether distribution is narrow or broad with respect to the sampled habitats. This aspect was examined using the sign test (see Methods), and the results, as expected, show fewer differences between species pairs (approximately 9% of all pairwise comparisons) than the Kolmogorov-Smirnov two-sample test (Table 2). The differences (see Table 2) tended to occur between species whose captures were widely distributed among the sampled habitats (e.g., Wood Thrush [WOTH], Swainson's Thrush, Ovenbird [OVEN], Hooded Warbler [HOWA], Kentucky Warbler), and species whose captures occurred primarily in younger second growth ("Traill's" Flycatcher [TRFL], Wilson's Warbler, Yellow-breasted Chat [YBCH], Indigo Bunting).

Of the 1339 individuals whose age was determined with certainty, 64.97% were immature, or first-year birds.

DISCUSSION

Coexistence among species in stable avian communities (e.g., breeding, wintering) occurs because individuals of each species are able to exploit different aspects of locally available resources (resource dimensions of the niche). In multidimensional niche space, each species in a stable community would occupy its own general area. This may not be true of migrants at stopover sites because of the ephemerality of these communities and the possibility that local resources are not needed or used by some of the communities' temporary members. Given also that more species occur at a stopover site during the migratory period than at any other time, there is great potential for species overlap in niche space. We do not know the degree to which this multidimensional space may or may not be "partitioned."

Bairlein (1981, 1983) found evidence for species-level segregations corresponding to morphology at a Palearctic stopover site. The array of habitats sampled in my study is much narrower, however, and at a finer scale (within woodlands), we should expect results to be more ambiguous, particularly when the mist net is the tool used to examine distributions. In an array of only 36 nets, we expect that some species will show similar

TABLE 2

RESULTS OF STATISTICAL TESTS EXAMINING STANDARDIZED CAPTURE DISTRIBUTIONS BETWEEN SPECIES PAIRS[a]

	GCFL	TRFL	LEFL	GRCA	WOTH	SWTH	WEVI	REVI	MAWA	AMRE	WEWA	OVEN	KEWA	HOWA	WIWA	YBCH	INBU
GCFL	—	n.s.	n.s.	*	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	**	**	n.s.	n.s.	n.s.
TRFL	n.s.	—	n.s.	n.s.	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	**	**	n.s.	n.s.	n.s.
LEFL	n.s.	n.s.	—	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	**	*	n.s.	n.s.	n.s.
GRCA	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	n.s.	n.s.
WOTH	n.s.	*	n.s.	n.s.	—	n.s.	**	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	**	*	**
SWTH	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	*	*	n.s.
WEVI	n.s.	*	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	n.s.	n.s.	n.s.
REVI	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	*	**	*	n.s.	n.s.	n.s.
MAWA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
AMRE	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
WEWA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
OVEN	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	**	*	*
KEWA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	—	n.s.	***	**	**
HOWA	n.s.	[a]	n.s.	n.s.	n.s.	n.s.	n.s.	*	[b]	n.s.	n.s.	n.s.	n.s.	—	**	*	*
WIWA	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	*	—	n.s.	n.s.
YBCH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	[b]	n.s.	—	n.s.
INBU	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	—

[a] Above the diagonal are the results of a Kolmogorov-Smirnov 2-sample test, testing for differences between species' distributions on a net-by-net basis. Below the diagonal are the results of a sign test, which tests for differences in capture distributions by comparing, essentially, the breadth of occurrence among the 36 nets. See text. Names corresponding to species codes are given in Table 1. * = $P < 0.05$; ** = $P < 0.01$; *** = $P \leq 0.001$.

[b] $P = 0.054$.

distributions, regardless of whether they are coexisting under a regime of differential resource exploitation or whether they are simply co-occurring. Species which in this study appear similar in two-dimensional distribution may occupy different niche space, but determination of this will require consideration of other data, such as diet, foraging maneuvers, height of activity, etc. Observations of the species considered here (unpubl.) suggest that such differences exist and can be quantified. There is also some temporal segregation (e.g., the Kentucky Warbler is an early migrant, while the Wood Thrush is later). These are only 17 of the 137 species captured in autumn at this site, however, leaving a tremendous degree of complexity unconsidered in this avian community.

Selectivity.—It is possible that some migrants do not feed at a site, occupying only physical, three-dimensional space and not casting a shadow upon the resource dimensions of the local environment. This may occur, for example, in migration "waves," when large numbers of birds can be found at a site, often apparently not feeding (although evidence remains anecdotal). If individuals were not consuming resources, there would be little pressure to seek profitable foraging locations, and any selection existing would be due to factors such as predator avoidance, temperature, humidity, etc. Under this scenario, we should expect broad distributions among wooded habitats in woodland birds, with much overlap between species. The evidence considered here suggests that this type of situation is not occurring at this site, but that, instead, a rather high degree of species-specific distribution occurs (Table 2, Fig. 2). Other evidence from this site (Winker 1995) suggests that resource demand probably drives a considerable amount of the selectivity observed.

The nature of the selection.—Hutto (1985b) suggested that exploratory assessment of nonbreeding habitats may occur among migrants at the landscape and macrohabitat scales. The data considered here do not address the landscape level, but the lack of evidence for shifting distributions at the macrohabitat scale suggests that exploratory assessment is either very rapid (occurring on a time scale not detectable using mist nets opened at dawn) or limited to finer scales. We know that assessment occurs in migrants at stopover sites. Both intraseasonal (Bairlein 1981, 1983) and interseasonal (e.g., Hutto 1985a; Winker et al. 1992a, b) changes in distribution suggest resource tracking (although interseasonal changes may be intertwined with endogenous selection criteria which themselves change seasonally). The within-day microhabitat distributional changes found at this site in the Kentucky Warbler are probably due to fine-scale resource tracking. On average, individuals of this species are gaining mass during the day at this site, and they seem to be depositing small to moderate amounts of fat (Winker 1995).

The lack of significant directionality in local movement (as reflected by side-of-capture data) corresponds well with my observations. Directional movements were commonly observed during the day in diurnal migrants of the families Accipitridae, Cathartidae, Apodidae, Columbidae, and Hirundinidae, but not among nocturnal migrants (unpubl. data). The absence of evidence for macrohabitat sampling and subsequent settling corresponds with stopover data in Germany (Bairlein 1981, 1983; Berthold 1989) and also supports my field observations. Despite hundreds of hours of observation in this area during autumn migration, I have not seen behaviors suggesting macrohabitat switching (or sampling and settling) as described by other investigators (e.g., Moore et al. 1990, Wiedner et al. 1992). This result underscores the likelihood that migrants can behave differently when right *on* the Atlantic coast (as opposed to even slightly inland, as at this site).

The question of endogeneity.—The majority of captured individuals were in their first year, and had never experienced tropical rainforest. Yet a rather high degree of species-specific selectivity occurred among the available habitats. This, coupled with the fact that distributions tended not to change during the day, leads me to conclude that habitat selection in these species may be largely endogenous.

Choices of where to settle appear to be made very quickly; the process was not apparent in observational or netting data. Also, potential exposure to social factors during the day (e.g., learning) did not seem to cause distributional shifts. Apparently rapid selection, comparative stability in distribution during the day, and species-specific patterns were all found here in non-flocking, relatively inconspicuous birds, the majority of which were naive or inexperienced. Similar results at a stopover site in Germany led Bairlein (1981, 1983) and Berthold (1989) to conclude that habitat selection in many Palearctic-Paleotropic migrants was probably under endogenous control. This control is not entirely rigid, however. Bairlein (1983) found evidence that young birds were distributed somewhat differently than adults in two species. He surmised that although habitat selection may be largely innate in passerine migrants, some part of this selection process may be improved by learning. In this context it is interesting to note that in my study within-day change in microhabitat distribution occurred in only one species.

Habitat selection in migrants.—Perhaps because little work has been done on migrant habitat selection, there is disagreement about how these studies should proceed. For example, I suggest that Wiedner et al.'s (1992) recommendations regarding the study of habitat selection in transient migrants (e.g., beginning data gathering 2–3 h after sunrise) are premature. First, the phenomenon they describe—flights of nocturnal migrants ex-

tending well into daylight hours—probably occurs primarily near large ecological barriers. Secondly, waiting 2–3 h after sunrise to begin examining the distribution of individuals causes one to miss the most active period. The data-gathering and analytical methods used here (directionality and comparisons of distributions between different times of day) can adequately address the question of settling.

The important issue in migrant habitat selection, however, is whether (or to what degree) transient migrants are actually *using* available stopover habitats. The idea that migrant habitat selection can be adequately studied through censusing alone ignores the uniqueness of the stopover community: namely, high levels of mobility, the ability to store energy, and the consequent possibility of not being dependent upon a site for food resources. The abundance of a species occurring at a site does not appear to be correlated with the importance of a site for fat deposition (see Winker et al. 1992c, Winker 1995). Further, remarkable differences in apparent resource harvesting can occur among the most common species at a site (Winker et al. 1992c). Learning about and accounting for the differences that appear among these species will be crucial both for an understanding of the evolution of the Nearctic–Neotropic migration system and for the successful conservation of this diverse group.

ACKNOWLEDGMENTS

The Smithsonian Institution and the Chicago Zoological Society supported the study. G. de la Garza (SEDUE), Dr. E. Ezcurra (SEDESOL), and G. Pérez H. (Estación de Biología Tropical "Los Tuxtlas," Instituto de Biología, UNAM) kindly issued the necessary permits. F. Puebla provided excellent field assistance. R. L. Hutto, P. Kerlinger, M. V. McDonald, and J. H. Rappole gave helpful comments.

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WILSON ORNITHOLOGICAL SOCIETY ANNUAL MEETING

The Wilson Ornithological Society will hold its annual meeting from 4 to 7 May 1995 at the Fort Magruder Inn and Conference Center in Williamsburg, Virginia. Queries may be directed to: Ruth Beck, Dept. of Biology, College of William and Mary, Williamsburg, Virginia 23185.

Appendix I

Vegetation Structure of Sampled Habitats[a]

P1	12	2	5	1	0	1	0	0	24	43	90	22
P2	7	9	6	3	0	0	1	0	21	55	80	25
P4	11	7	5	1	1	0	1	0	29	45	75	22
P16	11	11	8	2	1	0	1	0	50	30	90	23
P8	11	3	6	3	0	0	1	0	42	30	90	22
P15	17	2	5	3	1	0	1	0	35	29	81	20
P17	8	7	5	2	1	0	2	0	38	30	90	22
P3	3	7	5	3	0	0	0	0	22	45	65	23
P6	11	5	3	3	0	0	0	0	31	40	80	20
P5	6	7	3	1	1	0	0	0	50	35	80	21
P11	8	4	4	2	1	0	0	0	36	50	80	22
P12	12	7	4	2	2	0	0	0	31	25	80	18.5
P13	16	12	6	3	2	0	0	0	54	45	75	22
P10	4	6	8	1	2	0	0	0	36	55	80	18
P18	10	13	7	0	3	0	0	0	48	70	85	17
P7	8	6	2	0	0	0	1	1	38	40	95	19
P9	5	9	1	2	1	0	0	1	54	50	85	25
P14	17	5	4	1	0	0	0	1	60	55	86	25
A21	20	6	0	0	0	0	0	0	98	70	65	10
A27	23	4	1	0	0	0	0	0	122	70	65	12
A24	16	8	0	0	0	0	0	0	156	65	65	10.5
A25	19	6	0	0	0	0	0	0	167	65	55	7.5
A22	23	10	0	0	0	0	0	0	162	55	75	10.5
A32	23	7	0	0	0	0	0	0	122	50	75	9.5
A38	16	10	1	0	0	0	0	0	130	52	81	13.5
A35	16	11	2	1	0	0	0	0	66	55	60	12
A34	18	2	0	0	0	0	0	0	217	45	60	4.5
A23	14	2	0	0	0	0	0	0	161	70	45	6.5
A28	5	3	1	0	0	0	0	0	136	75	55	7
A30	4	1	0	0	0	0	0	0	131	80	65	6
A31	19	19	1	0	0	0	0	0	123	48	86	13
A36	26	22	3	1	0	0	0	0	92	38	86	14.5
A33	27	13	3	0	0	0	0	0	113	50	68	11.5
A37	30	12	5	0	0	0	0	0	96	38	90	14
A26	6	3	1	0	0	0	0	0	196	95	10	6.5
A29	5	0	0	0	0	0	0	0	344	70	15	5.5

[a] Columns are (1) net number; (2–9) number of trees in each size class (A–H); (10) number of "shrub" stems; (11) percent ground cover; (12) percent canopy cover; (13) canopy height (m). Rows (nets) correspond from top to bottom with the dendrogram in Fig. 1 (left to right).

Wilson Bull., 107(1), 1995, pp. 40–54

A COMPARISON OF BIRD COMMUNITIES IN BURNED AND SALVAGE-LOGGED, CLEARCUT, AND FORESTED FLORIDA SAND PINE SCRUB

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ABSTRACT.—We hypothesized that similar bird assemblages will occur in like-structured habitat that results from both clearcutting and high-intensity wildfire followed by salvage logging. To test this, we compared bird communities of sand pine scrub in mature forest and three disturbance treatments (1) high-intensity wildfire, salvage logged, and naturally regenerated, (2) clearcut, roller chopped, and broadcast seeded, and (3) clearcut and bracke-seeded. We analyzed communities based on residency status and nesting guilds. Migratory breeding birds were nearly restricted to mature forest. Bird communities of mature forest were significantly more species rich and diverse than those of disturbance treatments in spring. However, species richness and diversity of migratory winter residents did not differ among treatments, indicating that they are habitat-structure generalists on their wintering grounds. Canopy- and cavity-nesters and canopy- and bark-foraging species were virtually restricted to mature forest. Most species recorded in mature sand pine forest or disturbance treatments were either habitat-structure generalists or also occurred in other similarly structured vegetation types. However, the threatened and endemic Florida Scrub Jay (*Aphelocoma c. coerulescens*) occurred only in disturbance treatments (no differences). Silvicultural disturbance appears to mimic the natural high-intensity disturbance regime by creating habitat structural features required by open scrub species and may be an important habitat management tool where the use of wildfire is impractical. However, long-term effects, unsalvaged burns, and landscape patterns created by clearcutting were not addressed and may also be important in structuring bird communities of sand pine scrub. *Received 5 Jan. 1994, accepted 22 Aug. 1994.*

The influence of vertical and horizontal vegetation structure on bird communities is well known (MacArthur and MacArthur 1961, Cody 1968, James and Wamer 1982, Brown 1992). Natural disturbance plays a critical role in structuring habitat (Mushinsky and Gibson 1991). The impact of natural disturbance varies among ecosystems (Bormann and Likens 1979) in conjunction with the intensity, frequency, type, and size of the disturbance (Miller 1982).

Sand pine (*Pinus clausa*) scrub is a sclerophyllous, shrub-dominated ecosystem occurring on xeric, infertile sand (Kalisz and Stone 1984) in Florida and extreme southern Alabama. The shrub layer is dominated by

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myrtle oak (*Quercus myrtifolia*), sand live oak (*Q. geminata*), Chapman's oak (*Q. chapmanii*), crookedwood (*Lyonia ferruginea*), and two species of palmetto (*Serenoa repens* and *Sabal etonia*). Herbaceous groundcover is scant. The canopy is limited to a single species—sand pine.

Historically, low frequency, high-intensity, and large-scale wildfire created a temporally shifting age-class mosaic in peninsular sand pine scrub (Bartram 1791, Rawlings 1933, Webber 1935, Myers 1990). Semi-serotinous sand pine cones release copious quantities of seed (>2.47 million/ha) following high-intensity wildfire (Cooper et al. 1959), naturally creating often vast areas of even-age, monospecific sand pine stands. An open, shrub-dominated habitat was maintained between wildfires, while mature forest existed intermittently in time and space, especially on protected sites.

The avifauna of sand pine scrub has low endemism (Woolfenden 1969, 1970; Breininger and Schmalzer 1990). Only the threatened and endemic Florida Scrub Jay (*Aphelocoma c. coerulescens*) is restricted to scrub. Within scrub, jays inhabit only short-statured, oak-dominated habitat with patches of bare sand (Breininger 1981, Woolfenden and Fitzpatrick 1984). This habitat structure is available between approximately 3–15 years post-disturbance.

The Ocala National Forest in central Florida contains the largest remaining area of the endangered sand pine scrub ecosystem. Most has been lost to citrus or urban development (Myers 1990). Current forest management of sand pine scrub in the Ocala National Forest entails clearcutting patches of approximately 8–24 ha commonly followed by either roller chopping (nearly 100% soil surface disturbance) or bracke seeding, which creates small seed beds disturbing about 30% of the soil surface (Outcalt 1990). Because of the wood fiber value and the possibility of large-scale, uncontrolled burns, fires in sand pine stands are usually extinguished as rapidly as possible. Normally, burned sites are salvage-logged.

Plant community recovery and the subsequent habitat structure in clearcuts is similar in many respects to that following high-intensity wildfire (Abrahamson 1984a, b; Schmalzer and Hinkle 1992). Major differences include the presence of relatively few standing trees or snags for at least five years following wildfire, more slash piles, and less bole-sized woody debris in clearcuts versus burned sites (pers. obs.). Landscape patterns such as patch size and connectivity also differ between the two disturbance types.

Where the use of high-intensity wildfire is unfeasible for safety and economic reasons, other tools for maintaining early successional habitat must be sought. We predicted that bird assemblages would respond sim-

ilarly to habitat structure resulting from high-intensity disturbance regardless of means. We tested this hypothesis by comparing bird communities of clearcuts and of catastrophically burned, salvage-logged sites.

METHODS

We sampled the habitat structure of sand pine scrub in five replicate sites for each of three, 5- to 7-year-old disturbance treatments and mature forest. Treatments were (1) high-intensity burn, salvage logged, and naturally regenerated (HIB); (2) clearcut, roller chopped, and broadcast seeded (RC); and (3) clearcut and bracke seeded (BK). Mature (≥55 years), virgin sand pine stands that had been naturally regenerated following a stand-replacing fire in 1935 were used as the "control" treatment (MF).

Sand pine height and density were measured in five 10 × 10-m quadrats per site. Percent cover of shrub, bare ground, and herbaceous plants were measured using three 10-m line transects randomly placed within each quadrat.

We sampled birds in three replicate sites for each treatment. Three strip transects (20 × 250 m) were randomly established on each site (O'Meara et al. 1985), spaced a minimum of 100 m (plus a randomly chosen distance) apart. Transect locations were influenced by stand shape and size; all were a minimum of 50 m from stand or roadside edges except where prohibited by stand shape (two transects came within 20 m of edges for short distances). Transect width was restricted to 20 m to minimize variation due to visibility among sites and differences in detectability among species or season (detectability was greatly reduced in winter) (Emlen 1971, Robbins 1978). Narrow transect widths also increased the likelihood of detecting and distinguishing among individuals. Some species using treatment sites were not recorded within transects, but these generally were species that rarely used sites or those traveling in winter flocks beyond transect boundaries. This method standardized comparisons among treatments and overall appeared to reflect accurately the community composition.

We surveyed birds during breeding season (19 May–29 June) and winter (3 January–13 February) for two years (spring 1991 through winter 1993). Counts were conducted on each transect of each site four times during each season (Conner and Dickson 1980) by walking along the center line of the transect at approximately 20 m per minute while recording all birds seen or heard within 10 m in all directions. All surveys were terminated within three hours after sunrise. We rotated the sequence of surveys such that each site was sampled at least once during each of the 3 h following sunrise, and surveys were distributed throughout each season.

We recorded birds only if observed within transect boundaries. Birds flying over transects but not specifically using a study site were excluded, whereas others such as Tree Swallows (*Tachycineta bicolor*) and Common Nighthawks (*Chordeiles minor*) that were foraging above a transect were included. (Scientific names in text only for species not included in Table 2.) Similarly, birds using a site beyond the transect width which then flew over the transect and again landed beyond the boundary but within the site were included. Turkey Vultures (*Cathartes aura*) using air currents above transects for patrolling were excluded from analysis since we considered the air current rather than the stand itself to be the attractant.

For statistical analyses, we pooled data from transects within sites. For each season we averaged over repeated samples (four) and years (two) within sites such that site (N = 3) was the replicate unit. We calculated bird density based on absolute area surveyed and converted to numbers/km^2. We compared densities of each bird species among treatments for each season using one-way analysis of variance (ANOVA). We used fixed-effect, two-

TABLE 1

MEAN (±SE) STRUCTURAL CHARACTERISTICS OF SAND PINE SCRUB HABITAT IN THREE TREATMENTS AND MATURE FOREST, OCALA NATIONAL FOREST, FLORIDA

Treatment	Percent cover				Density (stems/ha) Pine	Height (>1 m) Pine
	Pine	Shrub	Herb	Bare ground		
Burn (HIB)	55.38	47.79	8.76	16.67	4860.00	2.87
	(7.51)	(2.33)	(1.49)	(1.20)	(344.87)	(0.09)
Chop (RC)	42.44	45.40	15.73	20.93	3680.00	2.77
	(5.90)	(1.27)	(5.08)	(1.25)	(716.19)	(0.16)
Bracke (BK)	23.64	53.15	5.78	22.76	3373.33	1.79
	(3.81)	(1.21)	(0.14)	(5.06)	(777.55)	(0.30)
Mature (MF)	87.38	78.53	28.95	0.00	691.67	17.12
	(0.60)	(3.32)	(7.94)	(0.00)	(58.05)	(0.56)

way ANOVA to compare species richness, Shannon's diversity indices (Shannon 1948), and total bird densities among treatments and seasons. If season-treatment interaction was significant, we used pairwise contrasts between least square means from the split-plot ANOVA to determine season effects (if significant) and one-way ANOVA to determine treatment effects within seasons. Data were log-transformed when required to correct for nonnormality or heteroscedasticity. We computed Horn's Index of Community Similarity (Horn 1966) for all possible treatment pairs during both winter and spring and also to compare winter and spring bird communities within treatments.

We assigned species to residency status groups as well as to nesting guilds (Root 1967) to test for differences among treatments and/or seasons using two-way and one-way ANOVA, as described above. Residents were classified as permanent, breeding only, or winter only. Nesting guilds were defined as ground-, shrub-, cavity-, and canopy-nesters (Harrison 1975).

RESULTS

Habitat structure differed considerably between mature forest and disturbance treatments (Table 1). Pine density was strikingly lower and tree height greater in MF relative to disturbance treatments. Shrub and herbaceous plant cover also were higher and bare ground cover lower in MF relative to disturbance treatments. The scale of structural differences among disturbance treatments was small relative to differences between MF and the treatments. Herbaceous cover was dominated by lichens in MF and by vascular plants in early-successional stands (Greenberg, unpubl. data).

Differences in bird communities corresponded with habitat structure rather than with treatment per se. Vegetation structure, along with bird species composition (Table 2), richness and diversity (Table 3), and com-

TABLE 2

MEAN SPRING AND WINTER DENSITY (UPPER NUMBER) ± SE (LOWER NUMBER) PER KM² OF SELECT SPECIES OF BIRDS IN THREE TREATMENTS AND MATURE FOREST IN SAND PINE SCRUB

Species (code)[a]	Spring				Winter			
	Burn (HIB)	Chop (RC)	Bracke (BK)	Mature (MF)	Burn (HIB)	Chop (RC)	Bracke (BK)	Mature (MF)
Downy Woodpecker (PC)	X		X	19.5	X	X	5.6	16.7
(*Picoides pubescens*)				12.1			2.8	4.8
Northern Flicker (PC)	2.8	5.6	2.8	X	2.8	2.8	22.2	0.0
(*Colaptes auratus*)	2.8	5.6	2.8		2.8	2.8	7.4	
Red-bellied Woodpecker (PC)	X	X	2.8	5.6	X	2.8	X	8.3
(*Melanerpes carolinus*)			2.8	5.6		2.8		4.8
Great Crested Flycatcher (BC)	X	X	X	41.7				
(*Myiarchus crinitus*)				26.8				
Blue Jay (PT)	5.6	X	X	11.1	8.3	8.3	2.8	2.8
(*Cyanocitta cristata*)	5.6			2.8	4.8	8.3	2.8	2.8
Scrub Jay (PS)	22.2	19.5	16.7		X		27.8	
(*Aphelocoma coerulescens*)	12.1	12.1	9.6				14.7	
Ruby-crowned Kinglet (W)					25.0	11.1	16.7	72.2
(*Regulus calendula*)					0.0	5.6	4.8	29.0
Blue-gray Gnatcatcher (PT)	X	13.9	5.6	50.0	2.8	0.0	0.0	36.1
(*Polioptila caerulea*)		7.4	2.8	12.7	2.8			20.0
Brown Thrasher (PS)	5.6	41.7	2.8	X	X	2.8	2.8	X
(*Toxostoma rufum*)	5.6	17.4	2.3			2.8	2.8	
American Robin (W)					19.4	36.1	86.1	97.2
(*Turdus migratorius*)					5.6	23.7	46.7	97.2
Yellow-throated Vireo (BT)			X	5.6				
(*Vireo flavifrons*)				5.6				
White-eyed Vireo (PS)	X	102.8	5.6	13.9	2.8	27.8	2.8	13.9
(*V. griseus*)		75.5	5.6	5.6	2.8	14.7	2.8	7.4

TABLE 2
CONTINUED

Species (code)[a]	Spring				Winter			
	Burn (HIB)	Chop (RC)	Bracke (BK)	Mature (MF)	Burn (HIB)	Chop (RC)	Bracke (BK)	Mature (MF)
Palm Warbler (W)					33.3	52.8	41.7	36.1
(*Dendroica palmarum*)					4.8	7.4	14.4	32.0
Pine Warbler (PT)				19.4	13.9	X	2.8	225.0
(*D. pinus*)				10.0	5.6		2.8	55.5
Yellow-rumped Warbler (W)					75.0	30.6	166.7	47.2
(*D. coronata*)					44.1	12.1	145.9	26.5
Common Yellowthroat (PS)	X	30.6	2.8		2.8	8.3	27.8	0.0
(*Geothlypis trichas*)		16.9	2.8		2.8	4.8	5.6	
Northern Cardinal (PS)	58.3	13.9	27.8	8.3	55.6	8.3	111.1	16.7
(*Cardinalis cardinalis*)	4.8	7.4	13.9	4.8	10.0	8.3	48.2	4.8
Rufous-sided Towhee (PS)	286.1	419.4	300.0	147.2	197.2	372.2	336.1	111.1
(*Pipilo erythrophthalmus*)	36.4	38.6	16.7	15.5	36.4	124.0	26.5	19.5
Summer Tanager (BT)	0.0	0.0	0.0	16.7				
(*Piranga rubra*)				4.8				

[a] Species code adheres to the following pattern. First letter, residency status—B = breeding resident; P = permanent resident; W = winter resident. Second letter, nesting guild (location of nest)—C = cavity; G = ground; S = shrub; T = tree. X indicates species was observed within a study site but was not recorded within transects.

TABLE 3

MEAN SPRING AND WINTER BIRD DENSITY, SPECIES RICHNESS, AND SHANNON'S DIVERSITY INDICES (±SE) IN THREE TREATMENTS AND MATURE FOREST IN SAND PINE SCRUB

Treatment	Density/km²	Richness	Diversity (H')
		Spring	
Burn (HIB)	388.9 ± 34.8	4.7 ± 0.3[a]	0.37 ± 0.03[a]
Chop (RC)	580.6 ± 59.8	6.3 ± 0.3[a]	0.43 ± 0.05[a]
Bracke (BK)	372.2 ± 20.0	5.3 ± 0.3[a]	0.32 ± 0.04[a]
Mature (MF)	372.2 ± 40.4	11.5 ± 1.5[b]	0.75 ± 0.06[b]
F	1.05	15.57	19.57
P	0.420	0.0005	0.0005
df	3	3	3
		Winter	
Burn (HIB)	530.6 ± 60.9	12.0 ± 1.0	0.84 ± 0.00[a,b]
Chop (RC)	594.4 ± 121.8	10.3 ± 1.2	0.61 ± 0.07[c]
Bracke (BK)	894.4 ± 207.5	11.0 ± 1.2	0.73 ± 0.03[a,c]
Mature (MF)	705.6 ± 140.8	11.7 ± 1.8	0.87 ± 0.02[b]
F	1.05	0.032	8.77
P	0.420	0.811	0.007
df	3	3	3

[a,b,c] Different letters within a column denote significant differences among treatments ($P < 0.05$). Data log-transformed for ANOVA.

TABLE 4

HORN'S INDEX OF COMMUNITY SIMILARITY (R_0) FOR SPRING AND WINTER BIRD COMMUNITIES IN THREE TREATMENTS AND MATURE FOREST IN SAND PINE SCRUB[a]

	Burn (HIB)	Chop (RC)	Bracke (BK)
		Spring	
Burn (HIB)			
Chop (RC)	0.862		
Bracke (BK)	0.947	0.929	
Mature (MF)	0.594	0.641	0.655
		Winter	
Burn (HIB)			
Chop (RC)	0.807		
Bracke (BK)	0.848	0.828	
Mature (MF)	0.686	0.606	0.653

[a] Values closer to 1.0 indicate greater community similarity between treatments.

TABLE 5

HORN'S INDEX OF COMMUNITY SIMILARITY (R_0) FOR WINTER VS SPRING BIRD COMMUNITIES IN THREE TREATMENTS AND MATURE FOREST IN SAND PINE SCRUB[a]

	Winter			
Spring	Burn (HIB)	Chop (RC)	Bracke (BK)	Mature (MF)
Burn (HIB)	0.669			
Chop (RC)		0.782		
Bracke (BK)			0.738	
Mature (MF)				0.583

[a] Values closer to 1.0 indicate greater community similarity between treatments.

munity overlap (Table 4) were significantly different between MF and each of the disturbance treatments.

Species richness ($F = 39.24$, df = 1, $P = 0.0002$) and diversity ($F = 57.48$, df = 1, $P = 0.0001$) were higher in winter than in spring for all disturbance treatments but not in MF (Table 3). In spring, MF had significantly higher species richness and diversity than disturbance treatments. There were no treatment differences in species richness in winter, but diversity was significantly lower in RC than in HIB or MF.

Bird density was significantly higher in winter than in spring in BK and MF ($F = 11.01$, df = 1, $P = 0.011$), but there was no treatment effect (Table 3). Within treatments, Horn's Index of Community Similarity indicated seasonal differences in community overlap; differences were most marked in MF (Table 5).

Permanent residents were numerically dominant during the breeding season (Fig. 1). There were no treatment ($F = 2.21$, df = 3, $P = 0.165$) or seasonal ($F = 0.04$, df = 1, $P = 0.843$) differences in permanent resident densities. Among permanent residents, Rufous-sided Towhees were numerically dominant in both seasons, but numbers were proportionally lower in winter due to the influx of migratory winter residents.

Species richness of permanent residents did not differ between seasons ($F = 3.08$, df = 1, $P = 0.117$) (Fig. 2). Among treatments, MF contained higher species richness of permanent residents ($F = 4.81$, df = 3, $P = 0.034$) than HIB or RC (suggested for BK; $P = 0.072$). Permanent residents occurring primarily in MF included several woodpeckers and the Pine Warbler.

Density and species richness of breeding-only birds were significantly higher in MF than in disturbance treatments ($F = 3.65$, df = 3, $P = 0.037$ and $F = 17.22$, df = 3, $P = 0.0008$, respectively) (Figs. 1 and 2). Breed-

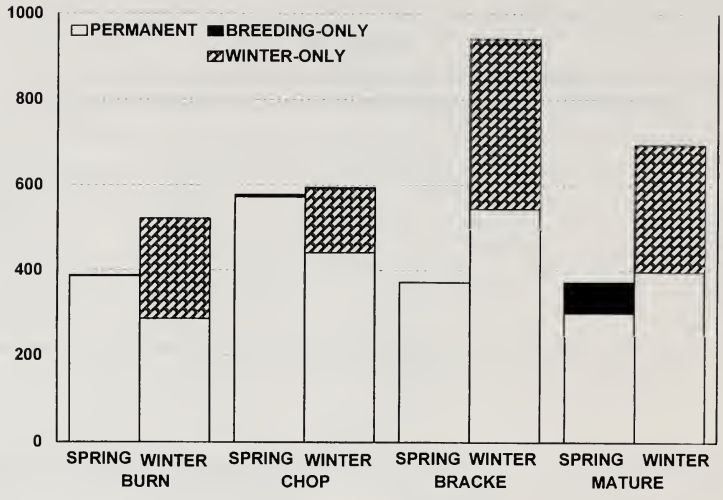

FIG. 1. Mean spring and winter density of permanent, breeding only, and winter-only residents in three treatments and mature forest in sand pine scrub.

ing-only species included the Great Crested Flycatcher, Summer Tanager, and Yellow-throated Vireo.

In winter, winter-only residents became numerically dominant (54–80% of total winter bird density). However, neither density nor species richness of this group differed among treatments or MF ($F = 0.83$, df = 3, $P = 0.512$ and $F = 0.65$, df = 3, $P = 0.606$, respectively) (Figs. 1 and 2). Common winter-only species included American Robin, Yellow-rumped Warbler, and Palm Warbler.

Nesting Guild

During the breeding season, treatment differences in species richness, composition, and relative densities of nesting guilds corresponded closely to habitat structure. Shrub-nesters (predominantly Rufous-sided Towhees) comprised >95% of total breeding bird density in all disturbance treatments and >45% in MF (Fig. 3).

Cavity nesters such as woodpeckers and the Great Crested Flycatcher, and canopy nesters such as the Blue-gray Gnatcatcher and Pine Warbler were also important in mature forest where tree boles and canopy provide additional niche dimensions. The density and species richness of canopy-nesting species were significantly higher in MF than in disturbance treat-

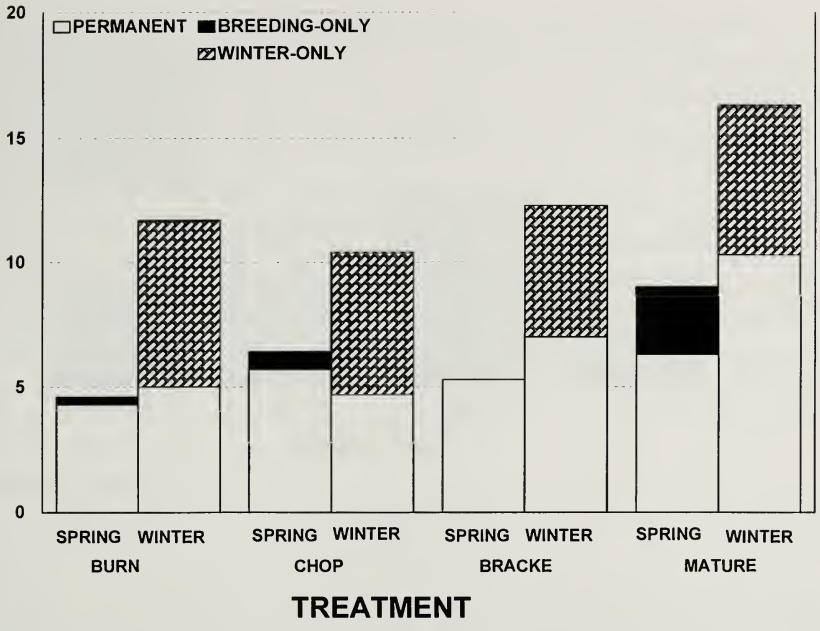

FIG. 2. Mean spring and winter species richness of permanent, breeding only, and winter-only residents in three treatments and mature forest in sand pine scrub.

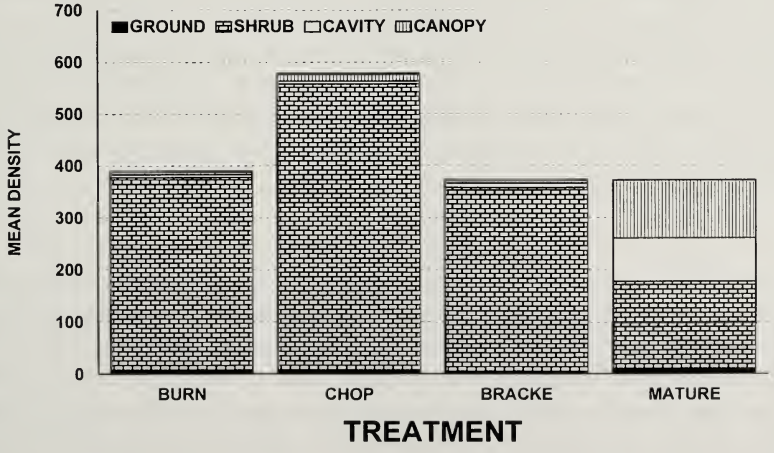

FIG. 3. Mean density of ground-, shrub-, cavity-, and canopy-nesting birds in three treatments and mature forest in sand pine scrub.

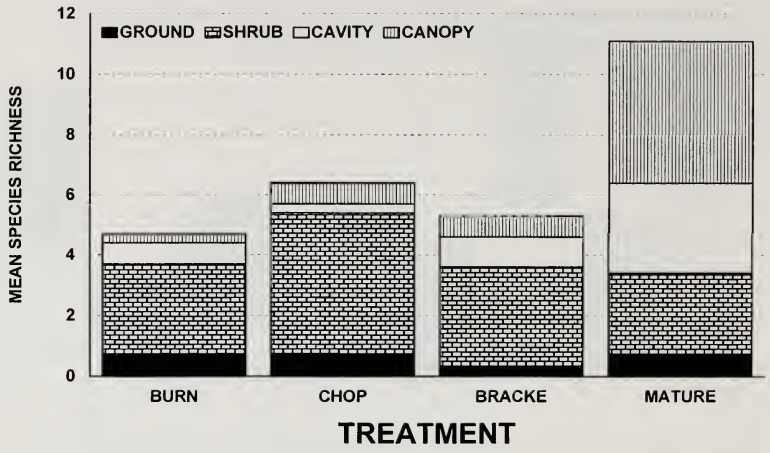

FIG. 4. Mean species richness of ground-, shrub-, cavity-, and canopy-nesting birds in three treatments and mature forest in sand pine scrub.

ments ($F = 4.37$, df = 3, $P = 0.042$ and $F = 21.86$, df = 3, $P = 0.0003$, respectively) (Figs. 3 and 4). Cavity nesters also tended to be more abundant ($F = 2.93$, df = 3, $P = 0.0995$) and species rich ($F = 3.04$, df = 3, $P = 0.093$) in MF than in disturbance treatments.

Conversely, fewer shrub-nesting species occurred in MF than in disturbance treatments, but more in RC than in HIB or BK ($F = 4.61$, df = 3, $P = 0.037$) (Fig. 4). Also, shrub-nesters were less abundant in MF than in disturbance treatments but more abundant in RC than in HIB or BK ($F = 35.89$, df = 3, $P = 0.0001$) (Fig. 3).

Neither density nor species richness of ground nesters differed among treatments ($F = 0.29$, df = 3, $P = 0.831$ and $F = 0.25$, df = 3, $P = 0.859$, respectively). Differences in occurrence and abundance of individual breeding bird species appeared to reflect differences in nesting habits (Table 2).

DISCUSSION

Our results support the hypothesis that similar bird communities occur in like-structured sand pine scrub habitat that results from high-intensity disturbance regardless of the means of disturbance. Because safety and economic considerations often prohibit the use of wildfire as a sand pine scrub management technique, clearcutting may be a viable way to create habitat for the Florida Scrub Jay and other scrub biota which depend on early successional scrub habitat.

Previous researchers (MacArthur and MacArthur 1961, Shugart and

James 1973, James and Wamer 1982) have demonstrated that bird species richness and diversity are positively correlated with increasing vertical and horizontal habitat structure. Our results also suggest that habitat structure governed most of the observed differences in species composition and diversity between MF and disturbance treatments. The presence of tall trees in MF provided additional foraging and nesting locations in and on tree boles and canopy. Community differences were especially apparent during the breeding season.

However, habitat structure appeared to be less important in winter. Although permanent MF residents such as most woodpeckers retained their forest association in winter, many winter-only birds such as Yellow-rumped Warbler, Palm Warbler, American Robin, Ruby-crowned Kinglet, House Wren (*Troglodytes aedon*), and Eastern Phoebe (*Sayornis phoebe*) appeared to be habitat-structure generalists on their sand pine scrub wintering grounds.

Our study was hampered by the absence of a true disturbance "control" (unsalvaged burn). By attracting such species as the Great Crested Flycatchers and woodpeckers, snag retention in high-intensity burns would likely have increased bird diversity for as long as they remained standing. Dead standing trees provide perching, nesting, and foraging sites for birds and attract insect prey (Conner 1978). Breininger and Smith (1992) found a positive correlation between woodpeckers and snag density in coastal scrub.

Bird species composition in our study was similar to that found in structurally similar scrub habitats (Woolfenden 1969, 1970; FGFWFC 1976; Breininger and Schmalzer 1990). Our density estimates were similar to Woolfenden's (1969, 1970) but lower than those reported by Breininger and Schmalzer (1990). Breininger and Schmalzer (1990) suggest that high bird densities in coastal versus interior (Woolfenden 1969, 1970) scrub result from differences in vegetation structure and composition, soil moisture, productivity, or geographical location. Population fluctuations among years as well as differences in density estimates resulting from survey techniques must also be considered.

Our data support the hypothesis that clearcutting mimics high-intensity burns that are followed by salvage-logging and in the short term does not appear to threaten the characteristic bird community of open sand pine scrub. Where natural disturbance processes are incompatible with other management objectives, clearcutting (with qualifications, such as increased snag and shrub retention) large patches of sand pine scrub on 50-year rotations may maintain suitable habitat for both forested and nonforested scrub bird communities. Fifty-year rotations approach the natural longevity of sand pine and probably mimic the average return interval of

high-intensity wildfire in sand pine scrub (Myers 1990). Long rotations will enhance diversity by providing a succession of habitats for migratory breeding birds and will ensure a "sustainable yield" of age-class or structure-class habitat availability for both open-scrub and forested sand pine scrub bird communities.

The limited scope of our study warrants cautious interpretation and implementation of our results. Further study is required to evaluate and improve ecosystem management in conjunction with forestry objectives in sand pine scrub. The long-term effects within and spanning several rotations of site degradation resulting from intensive site preparation could have negative consequences for open scrub bird communities and should be studied further. We did not address the potentially critical roles of standing snags and coarse woody debris following high-intensity burns in sand pine scrub. Finally, landscape patterns created by clearcut patches (Harris 1984, Franklin and Forman 1987) differ in size and arrangement from the landscape mosaic created by natural disturbance and could affect bird populations.

ACKNOWLEDGMENTS

This study was supported by the USDA Forest Service Southeastern Forest Experiment Station, Intensive Management Practices Assessment Center. We thank the Ocala National Forest staff for cooperation and assistance. K. Babbitt, D. Gordon, S. R. Humphrey, L. R. Franz, and G. W. Tanner provided useful comments on an earlier version of the manuscript. S. Coleman and P. Outcalt provided technical assistance with the manuscript.

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SOUTHERN HEMISPHERE ORNITHOLOGICAL CONGRESS

The Southern Hemisphere Ornithological Congress will be held 5–9 October 1996, in Albany, Australia. The meetings are organized by the Royal Australasian Ornithologists Union and will focus upon southern hemisphere birds and their habitats. Subthemes will include conservation and management, impact of fire, breeding biology, studies of seabirds and waders, foraging behavior, and plant-bird interactions. Persons seeking additional information should contact Brian Collins, School of Environmental Biology, Curtin University of Technology, GPA Box U 1987, Perth, Western Australia 6001 (Phone: 619 351 7054; FAX: 619 351 2495; email: B.Collins@info.curtin,edu.au).

Wilson Bull., 107(1), 1995, pp. 55–63

WETLAND USE BY BREEDING AND POSTBREEDING FEMALE MALLARDS IN THE ST. LAWRENCE RIVER VALLEY

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Abstract.—We examined the use of wetland habitats by female Mallards (*Anas platyrhynchos* from March 1990 through July 1992 in the St. Lawrence River Valley, a focus area under the North American Waterfowl Management Plan. Female Mallards spent most of their time breeding in forested-live wetlands (40%) and postbreeding in forested-dead wetlands (35%). According to wetland availability data, breeding and postbreeding females indicated selectivity for emergent and scrub-shrub wetlands. During postbreeding, they used fewer ($\bar{x}$ = 2.6, ± 0.2 [SE]) individual wetlands of larger size ($\bar{x}$ = 192 ha ± 30 ha) compared to the breeding season ($\bar{x}$ numbers = 4.1 ± = 0.2, P = 0.003; $\bar{x}$ size = 101 ha ± = 15 ha, P = 0.001). Moreover, females typically spent the postbreeding season in the vicinity of, or within, their breeding wetlands, hence conservation must simultaneously address breeding and postbreeding requirements. Protection of wetland complexes that contain a diversity of habitat types of differing sizes is recommended. *Received 29 March 1994, accepted 1 Oct. 1994.*

Mallards (*Anas platyrhynchos*) are declining throughout their primary breeding range in the prairie pothole region of North America (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986). As prairie habitats are lost to agriculture, secondary breeding habitats in northern forests have become increasingly important to the continental population (Gilmer et al. 1975, Trost et al. 1987). However, outside of prairie pothole habitats, research on dabbling ducks in general, and Mallards in particular, is meager. Such lack of data is especially significant in the St. Lawrence River Valley (SLRV) because it contains some of the most pristine wetlands—70% of which are forested—remaining in the northeastern United States (U.S. Fish and Wildlife Service 1991) and is a focus area under the North American Waterfowl Management Plan (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986). Hence, information on seasonal patterns of wetland habitat use should assist in identifying priority measures designed for protecting these important habitats, as well as increasing our understanding of Mallard ecology. Further, although the Mallard is the most frequently represented duck species in the literature worldwide (Heitmeyer 1987), traditional waterfowl research and management favoring breeding and wintering periods have resulted in a relatively poor understanding of postbreeding populations and their habitats (Hoh-

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man et al. 1992). We designed this study to examine habitat use patterns by female Mallards during breeding and postbreeding seasons in the SLRV.

STUDY AREA AND METHODS

We conducted the study within a 126-km^2 portion of the SLRV in northern New York (75°15′W, 44°38′N). Topography there is flat with rolling hills, and elevation ranges from 76 to 122 m above sea level (Will et al. 1982). Landscape in the SLRV is 53% forested, 35% agricultural, 11% wetlands, and 1% human-made structures (Grover 1978). Wetland conditions are pristine and consist of diverse complexes of forested swamps, shrub swamps, emergent marshes, wet meadows, farm ponds, rivers, and streams (Barnes et al. 1990, U.S. Fish and Wildlife Service 1991). Geology is extensively described in MacClintock and Stewart (1965) and wetland vegetation in Geis et al. (1977).

We captured female Mallards from 23 March through 27 April, 1990–92, using decoy traps (Sharp and Lokemoen 1987), and attached a 20-g radio-transmitter dorsally to each bird using a harness (Dwyer 1972). We removed primary covert number two on each female and used black-and-white surface area (mm^2) and dry weight (mg) of this feather to determine age using an improved version (G. Krapu, pers. comm.) of the discriminant function initially published in Krapu et al. (1979).

We used a hand-held yagi antenna (3- or 4-element) and 150–151 Mz scanning receiver to "home in" on birds and locate them in particular wetland basins. Homing was the process by which we approached birds on foot or from a truck only until we could identify the individual wetland basin the bird was using. Our objective was to locate radio-marked females in individual basins delineated on U.S. Dept. of Interior, National Wetlands Inventory maps (1:24,000). We were not concerned with documenting subtle movements within individual wetland basins, so telemetry error was negligible (Frazer et al. 1990).

We relocated radioed females 4–7 days/week and attempted to locate all females on each day. Females not located on a particular day were given priority the following day to standardize tracking effort. Individual birds were located only once each day to control for autocorrelation bias (Swihart and Slade 1985). The breeding season was defined as the interval between the first and last egg laid during the year. Individual birds were assigned postbreeding status the following day or when we observed them in flocks, whichever came first. Telemetry began the third week of April and ended the last week in July.

We studied the six major types of palustrine wetlands used by Mallards on our study area: forested-live, forested-dead, scrub-shrub, emergent, farm pond, and river. Forested-live types were dominated by living broad-leaved deciduous trees, primarily red maple (*Acer rubrum*), American elm (*Ulmus americana*) and ash (*Fraxinus* spp.). Forested-dead types were dominated by dead trees, but were similar to forested-live wetlands in species composition. Scrub-shrub types were dominated by deciduous broad-leaved shrubs, mainly speckled alder (*Alnus rugosa*), willow (*Salix* spp.), silky dogwood (*Cornus amomum*), and meadowsweet (*Spirea alba*). Emergent types were dominated by narrow-leaved persistent herbaceous vegetation, principally sedge (*Carex* spp.), cattail (*Typha* spp.), bulrush (*Scirpus* spp.), and spike rush (*Elocharis* spp.). Farm pond types were small (<11 ha) open water wetlands created and maintained by people. River types were open water wetlands with channels of high gradients and velocity.

We divided the study area into 1-km^2 blocks and used only blocks that contained ≥1 radio-location for each year. We used an electronic digitizer to measure the area of all wetland basins that fell within boundaries of study area blocks and individually coded each basin. Percent composition of wetland types was determined separately for each 1-km^2 block.

Study areas were 69 km² (i.e., 69 blocks) in 1990, 84 km² in 1991, and 81 km² in 1992, and pooled size over three years was 126 km². Only 42 (33%) of the 126 study area blocks were shared among all three years, 24 (19%) between two years, and the remaining 60 (48%) were unique to a given year. However, despite low overlap in blocks among individual years, percent composition of wetland types was nearly identical for yearly study areas, and the greatest difference between any two years was 6% for forested-live wetlands. Percent wetland habitat covering the yearly study areas was 32.8% in 1990, 32.3% in 1991, and 31.0% in 1992, respectively.

For each bird at each location, we recorded the type and size of the individual wetland basin. Number of wetlands used by each female was the total number of different wetland basins where we obtained at least one location. Percent use of each wetland type was calculated for each female by dividing the number of locations in each wetland type by the total number of locations; for analysis, percent use data were normalized by arcsine transformation. Size of individual basins was averaged to yield a mean wetland size for each bird during each season; for analysis, wetland size data were weighted by the number of locations obtained in individual basins.

We used one-way analysis of variance to test for yearly differences in percent use of different wetland types, mean wetland size, and number of wetlands used during each season. We used unpaired *t*-tests to test for differences in habitat use between breeding and postbreeding seasons and between ASY and SY females. Data were managed and analyzed using PC SAS (SAS Institute 1988).

RESULTS

We radio-marked 128 female Mallards over three years (44 in 1990, 44 in 1991, 40 in 1992). We omitted from analysis 31 birds that either disappeared within two weeks of marking, were found dead upon first radio-location, dropped their radios, or wore defective radios. The breeding sample, therefore, included 97 females (41 ASY, 52 SY, 4 unknown age) that we separated into individual year-age data sets. The postbreeding sample, also divided into separate year-age data sets, was reduced to 74 females (32 ASY, 39 SY, 3 unknown age) after accounting for birds that disappeared or died during the breeding season.

Wetland use was similar ($P > 0.05$) between ASY and SY females, within and between seasons, so we pooled the data on age class (including birds of unknown age) and tested for differences among years and between breeding and postbreeding seasons. Analysis was based upon 1670 breeding season radio-locations (367 in 1990, 666 in 1991, and 637 in 1992) and 1017 postbreeding radio-locations (307, 388, 322). Mean ($\pm$SE) number of locations obtained per bird over the three years was 16.6 ($\pm$0.94) during the breeding season (11.8 $\pm$ 1.2 in 1990, 21.8 $\pm$ 2.2 in 1991, 16.8 $\pm$ 1.2 in 1992) and 13.7 during the postbreeding season (14.0 $\pm$ 1.8, 17.6 $\pm$ 1.8, 10.7 $\pm$ 0.9).

Forested-live wetlands comprised 46–51% of the wetland area and were used by female Mallards 37–42% of the time during breeding and 23–28% during postbreeding; seasonal differences were evident ($P < 0.05$)

TABLE 1

PERCENT AREA AND USE OF SIX WETLAND HABITAT TYPES BY FEMALE MALLARDS DURING BREEDING AND POSTBREEDING SEASONS IN THE ST. LAWRENCE RIVER VALLEY, NORTHERN NEW YORK, 1990–1992[a]

Wetland type	Year	% Area	% Use		P^b
			Breeding	Postbreeding	
Forest-live	1990	47.2	41.6	27.8	0.13
	1991	51.2	42.3	22.7	0.02
	1992	45.6	37.4	24.5	0.06
	1990–1992	51.1	40.2	24.9	0.01
Forested-dead	1990	32.1	7.6	25.6	0.05
	1991	29.1	13.7	42.0	0.01
	1992	32.8	17.6	35.5	0.07
	1990–1992	25.3	13.3	34.5	0.01
Emergent	1990	6.2	28.9	27.9	0.82
	1991	4.6	20.0	5.9	0.01
	1992	9.0	21.5	18.8	0.55
	1990–1992	8.2	23.4	17.7	0.10
Scrub-shrub	1990	11.5	21.6	18.6	0.71
	1991	12.2	21.2	27.6	0.74
	1992	9.7	23.1	19.2	0.60
	1990–1992	12.1	22.1	21.5	0.73
Farm pond	1990	2.1	0.0	0.0	—
	1991	1.9	2.1	1.9	0.92
	1992	1.9	0.2	2.0	0.29
	1990–1992	1.5	0.7	1.4	0.51
River	1990	0.9	0.3	0.0	—
	1991	1.0	0.8	0.0	—
	1992	0.9	0.1	0.0	—
	1990–1992	1.9	0.4	0.0	—

[a] Yearly sample sizes (breeding, postbreeding) were 31, 22 females in 1990; 28, 22 in 1991; 38, 30 in 1992.
[b] *P*-values from *t*-tests comparing yearly wetland use between seasons.

during 1991 and overall (Table 1). Forested-dead wetlands comprised 25–33% of the wetland area and were used by female Mallards 8–18% of the time during breeding and 26–42% during postbreeding; differences between seasons were conspicuous ($P \leq 0.05$) during two of three years and overall. Emergent wetlands comprised 5–9% of the wetland area and were used by female Mallards 20–29% of the time during breeding and 18% during postbreeding. During 1991, use of emergent wetlands declined to a low of 6% during postbreeding ($P = 0.01$); otherwise, emergent wetlands were used at similar levels ($P > 0.05$) between seasons. Percent use of scrub-shrub wetlands was 22% during both seasons ($P >$

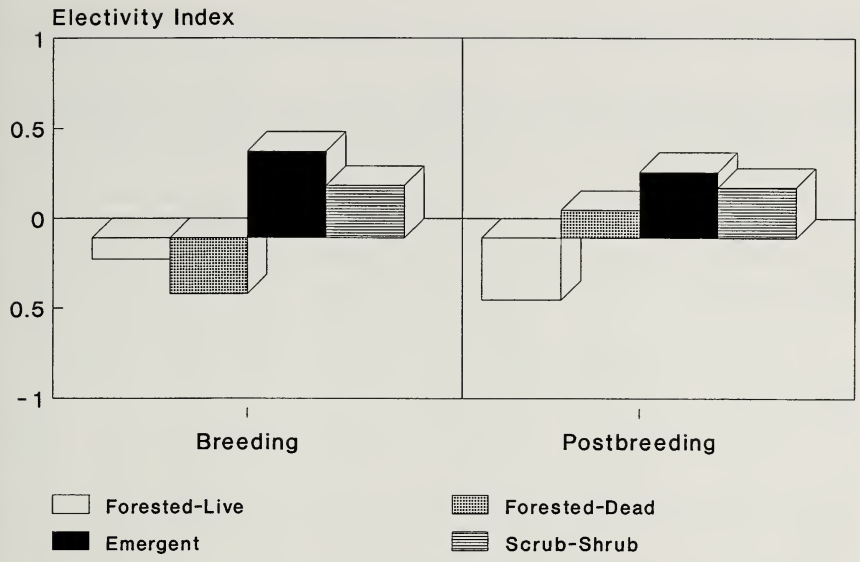

FIG. 1. Habitat electivity indices for female Mallards breeding and postbreeding in the St. Lawrence River Valley, northern New York, 1990–92. Sample sizes were 97 and 74 females for breeding and postbreeding seasons, respectively.

0.05), but these wetland types comprised only 10–12% of the wetland area. Use of farm pond and riverine wetlands was only 2%, but these wetland types comprised a small (≤2% each) proportion of the wetland area. Seasonal differences were small ($P \geq 0.05$), and in some years we did not locate postbreeding females in these wetland types (Table 1).

Seasonal use of wetland types did not differ ($P > 0.05$) among years; only postbreeding use of emergent wetlands approached significance among years ($F = 2.81$, 2 df, $P = 0.07$). To examine percent use data relative to percent availability data, we applied an electivity index (Ivlev 1961) to the pooled data, where indices <0 indicated low selection and indices >0 indicated high selection. Electivity analyses for the four major wetland types used revealed high selection indices for emergent and scrub-shrub wetlands and low indices for forested-live wetlands during both seasons (Fig. 1). Selection indices for forested-dead wetlands were low during breeding and high during postbreeding (Fig. 1).

Female Mallards generally used smaller wetland basins during breeding (84–124 ha) than postbreeding (120–246 ha), and seasonal differences were evident ($P < 0.05$) overall and in 1992 (Table 2). Female Mallards always used more ($P < 0.05$) wetland basins during breeding than postbreeding. For years pooled, mean (±SE) number of wetlands used by

TABLE 2

MEAN SIZE AND NUMBER OF WETLANDS USED BY FEMALE MALLARDS DURING BREEDING AND POSTBREEDING SEASONS IN THE ST. LAWRENCE RIVER VALLEY, NORTHERN NEW YORK, 1990–1992[a]

Variable	Year	Breeding season			Postbreeding season			P^b
		$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	
Wetland size (ha)	1990	84.3	22.4	2.4–584	193.6	59.3	0.4–729	0.06
	1991	87.1	25.2	0.8–605	120.0	29.2	1.2–533	0.40
	1992	124.2	26.4	0.4–729	245.5	54.4	0.8–729	0.04
	1990–1992	100.7	14.5	0.4–729	192.1	29.6	0.4–729	0.01
No. of wetlands	1990	3.8	0.27	1–8	2.8	0.34	1–7	0.02
	1991	4.9	0.47	1–10	3.1	0.36	1–8	0.01
	1992	3.9	0.33	1–10	2.2	0.27	1–8	0.01
	1990–1992	4.1	0.21	1–10	2.6	0.19	1–8	0.01

[a] Yearly sample sizes (breeding, postbreeding) were: 31, 22 females in 1990; 28, 22 in 1991; 38, 30 in 1992; 97, 74 1990–1992.

[b] *P*-values from t-tests comparing yearly means between seasons.

individual females during breeding was 4.1 (±0.21) and ranged from 1 to 10. During postbreeding, mean number of wetlands used declined to 2.6 (±0.19) and ranged from one to eight wetlands. There were no yearly differences ($P > 0.05$) in wetland size or number used during breeding and postbreeding.

DISCUSSION

Among ducks, Mallards breed in the greatest variety of habitats, and quantifying and describing their habitat patterns is often difficult (Bellrose 1976). Breeding and postbreeding female Mallards used all wetland habitats in the SLRV, but our assessment of the four most frequently used wetland types indicated that emergent and scrub-shrub types were selected above forested types of live- or dead-timber. High use of emergent and scrub-shrub wetlands during breeding and postbreeding suggests that these wetlands provide cross-seasonal benefits to female Mallards, especially during years of normal water levels. In 1991, for example, below normal rainfall and snowfall the preceding winter (NOAA, U.S. Dept. Commerce, Asheville, North Carolina) caused water levels to drop considerably (J. E. Lamendola, pers. comm.). That year, use of emergent wetlands by females declined to a low of 6% during postbreeding; otherwise, percent use of emergent wetlands always exceeded availability. In the densely forested Adirondacks, female Mallards also appeared to

select the scarcer emergent and scrub-shrub wetlands over forested wetlands (Dwyer 1992).

Mallards are relatively recent breeders in forested habitats of northeastern North America (Heusmann 1974), and forested wetlands comprised 76% of the wetland area in our study. At 53%, absolute use of forested wetlands (live- and dead-timber) appeared high, until examined in relation to the composition of forested wetlands. Our results complement studies of Mallard habitat use in forested wetlands in the Adirondacks (Dwyer 1992) and Minnesota (Gilmer et al. 1975), where high use was a function of high availability. However, use of forested-dead wetlands always exceeded coverage during postbreeding, particularly in the dry year of 1991. The seasonal shift to forested-dead wetlands during postbreeding probably was related to duration of moisture in these wetlands. For example, forested-dead wetlands were associated primarily with semi-permanent water regimes, whereas forested-live, emergent, and scrub-shrub wetlands were associated mostly with less permanent seasonal-saturated regimes (see Cowardin et al. 1979).

The functional role of wetland complexes for breeding dabbling ducks is related to wetland availability (Nudds and Ankney 1982). In early spring, small and less permanent wetlands were always first to thaw and yield invertebrates and were used intensively by pairs when larger wetlands were still frozen. We also observed females frequenting temporary water areas that formed in early spring from snow-melt water collected within small upland depressions. These were maintained by spring rains, their availability changed daily depending on air temperature, humidity, and rainfall, and they usually vanished by early May, when females entered larger wetlands and remained relatively sedentary for the remainder of the breeding season.

The most wetlands used by any female during the breeding season was 10 ($\bar{x}$ = 4.1), and some females used only one wetland basin during the entire breeding season. In forested wetlands of Minnesota, breeding females used 4–13 ($\bar{x}$ = 8.6) wetlands (Gilmer et al. 1975), and prairie-nesting females in North Dakota used seven to 22 ($\bar{x}$ = 15) wetlands (Dwyer et al. 1979). Fundamental differences between number of wetlands used in the SLRV and the aforementioned studies probably was related to wetland distribution and size (Nudds and Ankney 1982). For example, females in the North Dakota study used more wetlands, but wetland size averaged only 1.6 ha (Dwyer et al. 1979). In the SLRV, where wetland size averaged 9.5 ha (range = 0.04–867.3 ha), females apparently meet their breeding requirements within fewer wetland basins. However, postbreeding females used fewer and larger-sized wetlands than did breeding females. These seasonal changes were consistent from year

to year, and the larger wetlands probably were conducive to their molting ecology (e.g., restricted mobility) and flocking, postbreeding behavior.

Intensive management of wetland habitats using water level manipulation to change vegetation composition is difficult to propose for the SLRV, given that the large watersheds contain some of the most pristine and unpolluted wetlands remaining in the northeast United States (U.S. Fish and Wildlife Service 1991). We recommend protection of wetlands from human encroachment and associated threats of development as the best conservation strategy.

Habitat use data can provide insights into the selection and prioritization of habitats for protection. For example, our data indicated that wetland basins dominated by emergent and scrub-shrub vegetation were important to female Mallards during breeding and postbreeding. Protection of breeding habitat should also emphasize small nonpermanent wetlands and sheetwaters associated with agricultural fields that thaw before large permanent wetlands early in the breeding season. Further, female Mallards typically spend the postbreeding season in the vicinity of, or within, their breeding wetlands, so habitat protection should simultaneously address both periods.

ACKNOWLEDGMENTS

Financial support was provided by the U.S. Fish and Wildlife Service (Cooperative Agreement No. 14-16-005-89-9007) and Federal Aid in Fish and Wildlife Restoration (Project W-81-R) through the New York State Dept. of Environmental Conservation (NYSDEC), New York State Conservation Fund. Partial support was provided by the Adirondack Wildlife Program at the State Univ. of New York, College of Environmental Science and Forestry. We thank B. L. Swift and other NYSDEC personnel for logistical support; J. H. Smith for field assistance; and R. H. Brocke, R. E. Chambers, C. P. Dwyer, R. A. Malecki, and H. B. Underwood for reviewing an earlier draft of the manuscript. We are grateful to SLRV landowners for allowing us access to their land.

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Wilson Bull., 107(1), 1995, pp. 64–72

SPRING FEEDING ECOLOGY OF CINNAMON TEAL IN ARIZONA

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ABSTRACT.—I examined feeding behavior and diet of Cinnamon Teal (*Anas cyanoptera*) breeding on high-elevation (>1950 m) wetlands in northern Arizona to determine the dietary strategies this species uses to meet energy and nutrient demands from spring arrival through laying. Females spent more diurnal time feeding ($P < 0.001$) and contained more total food and a greater proportion (dry mass basis) of animal food ($P < 0.10$) than their mates. Invertebrate proportion of female diets varied ($P = 0.029$) among three reproductive categories (64–76%) and among three locations (64–85%), whereas male diets did not ($P = 0.179$). Aquatic dipterans and gastropods comprised 36% and 15% of female diets and 32% and 8% of male diets, respectively. Dietary strategies of Cinnamon Teal nesting on high-elevation wetlands in Arizona are similar to those of other *Anas* species breeding on prairie habitats. *Received 28 March 1994, accepted 2 Oct. 1994.*

Dabbling ducks (genus *Anas*) produce large clutches of eggs that have a high energy density and are large relative to female mass (King 1973). Females of most species rely to some extent on endogenous reserves acquired before or after arrival on breeding areas for the lipid component of clutch formation but use exogenous food sources to meet egg protein requirements (Alisauskas and Ankney 1992). To meet protein demands, females shift from a plant-dominated nonbreeding diet and forage intensively on protein-rich aquatic invertebrates prior to and during egg-laying (Krapu and Reinecke 1992, but see Wishart 1983). These data on dabbling duck feeding ecology are based primarily on studies conducted in the prairie pothole region, however, and may not reflect dietary patterns of populations or species breeding in other wetland landscapes (Krapu and Reinecke 1992).

The North American breeding range of the Cinnamon Teal (*A. cyanoptera*) is centered in the arid Great Basin and surrounding intermountain areas; a few pairs nest in the prairie pothole region (Bellrose 1980). In Arizona, Cinnamon Teal breed primarily on wetlands above 1950 m elevation, near the southern rim of the Colorado Plateau (Brown 1985). Early food habits studies indicated that breeding Cinnamon Teal rely primarily on plant foods (Mabbot 1920, Munro 1939, Martin et al. 1951, Spencer 1953), but these results are biased toward hard foods because contents of the gizzard, rather than the esophagus and proventriculus, were examined (Swanson and Bartonek 1970). I examined the diet and feeding behavior of Cinnamon Teal on high-elevation wetlands in Ari-

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zona. Based on studies of prairie-nesting *Anas* species, I predicted that paired females would spend more time feeding and feed to a greater extent on invertebrate foods than their mates and that diets of laying females would contain proportionately more animal foods than diets of pre-laying females. I also examined whether Cinnamon Teal diets differed among three sites differing in elevation and wetland habitat characteristics.

STUDY AREA AND METHODS

I studied Cinnamon Teal feeding ecology during March–June in 1992 and 1993 at three locations on the Colorado Plateau in northern Arizona: the Anderson Mesa, the White Mountains, and wastewater effluent wetlands located northwest of the White Mountains (see Brown 1985 and Piest and Sowls 1985 for detailed descriptions). On the Anderson Mesa (2100–2200 m elevation), Cinnamon Teal were most common on seasonal and semipermanent wetlands dominated by spikerushes (*Eleocharis* spp.), hardstem bulrush (*Scirpus acutus*), and smartweeds (*Polygonum* spp.). In the White Mountains (2500–2900 m elevation), Cinnamon Teal occurred primarily on large, semipermanent wetlands supporting water sedge (*Carex aquatilis*), manna grass (*Glyceria borealis*), and some bulrush and smartweeds. On two effluent marshes (1937 and 2048 m elevation), Cinnamon Teal fed in seasonally flooded habitats characterized by cattails (*Typha* spp.), bulrushes, spikerushes and a variety of annual seed-producing plants.

The two effluent wetlands and randomly selected wetlands on the Anderson Mesa (N = 40) and the White Mountains (N = 45) were censused weekly throughout the study period. Wetlands occupied by Cinnamon Teal were visited at least three times each week, and pairs on each wetland were randomly selected for 15-min focal time-activity sessions during early morning (one-half h before sunrise until 2 h after sunrise), mid-day (2 h after sunrise until 2 h before sunset), or late afternoon (2 h before sunset until 0.5 h after sunset) time periods. Each day, focal sessions were not conducted on the same pair more than once during any time period. Pair-bonds were identified before focal sessions, and verified during focal sessions, by the behavior of pair members toward each other and conspecifics. Behaviors (feeding or non-feeding) of both pair members were recorded at 10-sec intervals during each session.

I shot both members of 34 pairs (pair members were feeding <1 m from each other), and females from 18 additional pairs of Cinnamon Teal. All birds were observed feeding for >10 min before collection and contained >0.001 g (dry mass) of food. I removed the esophagus and proventriculus from each bird and stored them with their contents in 80% ethanol immediately after collection. I assigned females to the following reproductive categories: arrival/migrant—no developing ovarian follicles; RFG—≥1 follicle ≥6.0 mm and accumulating yolk, and no ruptured follicles; or laying—ruptured and developing follicles present. Males were assigned the reproductive status of their mate.

Food items from each bird were identified using standard references (Martin and Barkley 1961, Pennak 1978, Merritt and Cummins 1984), sorted, and dried (65°C) to constant mass. I calculated the aggregate percent dry mass (Swanson et al. 1974b) and frequency of occurrence of each food item for each sex, location, and reproductive status.

I used Wilcoxon signed-ranks tests (Daniel 1978) to make paired comparisons between sexes of (1) the percent time spent feeding by pairs during focal observations and (2) the proportion of animal foods in the diet and total dry mass of food contents in the 34 pairs of Cinnamon Teal I collected. For each sex (N = 54 females, 34 males), I used two-way ANOVA to test the effects of the independent variables reproductive category and location

on the dependent variable animal proportion of the diet (dry mass) and Tukey's studentized range test to compare means among groups (PROC GLM; SAS Institute Inc. 1987). Because small sample sizes increased the likelihood of type II errors, I used an alpha level of 0.10 for all comparisons.

RESULTS

Paired female Cinnamon Teal spent a greater ($P < 0.001$) percentage of diurnal time feeding than did their mates in 1992 (65% versus 52%, N = 259 focal sessions) and 1993 (56% versus 48%, N = 323). Females in all reproductive categories contained more ($P < 0.01$) food (plant and animal) than did their mates (Table 1). Arrival/migrant and laying female diets contained a greater proportion of invertebrates ($P < 0.01$) than did their mates; RFG female diets also contained higher proportions of animal food than did their mates, but this difference was not significant ($P = 0.14$) (Table 1).

The animal proportion of female diets differed among reproductive categories and locations (Table 1). Invertebrate proportion of laying female diets was greater than in RFG female diets ($P < 0.10$), but neither of these groups differed ($P > 0.10$) from the invertebrate content of arrival/migrant female diets. Diets of females collected on effluent marshes contained more ($P < 0.05$) animal matter than diets of females collected on White Mountain wetlands, whereas the invertebrate proportion of female diets on Anderson Mesa wetlands was similar to other locations ($P > 0.10$). Male diets did not differ among reproductive categories or collection locations (Table 1).

Aquatic dipterans (primarily Chironomidae larvae) and snails (Gastropoda) were the most important animal foods in the diet for each sex, reproductive category, and location, together comprising 51% and 41% of the diet of females and males, respectively (Table 2). Chironomids comprised 42% (females) and 46% (males) of the diet of Cinnamon Teal collected on effluent marshes but <14% of the diet of birds collected at other locations. Aquatic coleopterans and hemipterans together comprised 24% of the diet of laying females but <6% of arrival/migrant and RFG female diets.

Seeds were the most common plant foods consumed (Table 2), and taxa varied among collection locations in accordance with the dominant seed-producing plants in wetlands used by Cinnamon Teal. In the White Mountains, *Carex* seeds accounted for 44% and 63% of plant foods in the diet of females and males, respectively, whereas *Eleocharis* (57% and 30%) and *Scirpus* (23% and 45%) dominated the plant diet of Cinnamon Teal on the Anderson Mesa. On effluent marshes, *Eleocharis* (33%) and *Polygonum* (39%) seeds comprised the majority of plant foods in the diet

TABLE 1

DIET CHARACTERISTICS OF CINNAMON TEAL IN NORTHERN ARIZONA, 1992–1993

Location	Reproductive category				Statistical analyses[a]			
	Arrival/migrant	RFG	Laying	Combined	Source	*F*	df	*P*
Females								
Anderson Mesa	75.7[b] (8)[c]	41.2 (6)	71.0 (6)	64.1 (20)	Model[d]	2.96	8	0.03
White Mountains	36.4 (4)	54.3 (6)	68.1 (4)	52.2 (14)	Rep. status	2.37	2	0.10
Effluent wetlands	73.6 (9)	96.8 (6)	95.3 (3)	85.0 (18)	Location	4.50	2	0.02
Combined	67.3 (21)	64.4 (18)	75.7 (13)	68.3 (52)				
Males								
Anderson Mesa	48.0 (5)	25.5 (5)	27.2 (3)	32.1 (13)	Model	1.69	8	0.18
White Mountains	39.7 (2)	80.0 (5)	50.5 (2)	47.3 (9)				
Effluent wetlands	87.4 (4)	59.6 (6)	25.0 (2)	60.8 (12)				
Combined	60.7 (11)	55.3 (16)	33.2 (7)	52.5 (34)				
	0.031[e]	0.563	0.029					
Mates combined[f]	63.1 (11)	66.4 (16)	71.7 (7)					
	0.162	0.897	0.044					

[a] Based on ANOVA with type III sums of squares.
[b] Mean percent (dry weight) animal foods in diet.
[c] Sample size.
[d] A nonsignificant ($P > 0.1$) interaction term (reproductive category × location) was not included in this model.
[e] Mean dry mass (g) of all esophageal food contents (plant and animal).
[f] Mean percent animal foods and dry mass of total food contents for females paired to males in each reproductive category.

TABLE 2

AGGREGATE PERCENT DRY MASS AND PERCENT FREQUENCY OF OCCURRENCE OF FOOD ITEMS CONSUMED BY CINNAMON TEAL IN NORTHERN ARIZONA, 1992–1993

Food item	Females (N = 52)		Males (N = 34)	
	Dry mass	Occurrence	Dry mass	Occurrence
Diptera[a]	35.8	85	32.6	71
(Chironomidae)	(21.1)	(60)	(20.8)	(50)
Gastropoda[b]	15.5	33	8.4	24
Hemiptera[c]	5.5	29	3.0	15
Coleoptera[d]	4.0	19	3.5	9
Ephemeroptera	1.7	4	0.6	6
Amphipoda	1.6	4	0	0
Cladocera	1.1	12	2.0	12
Ostracoda	0.9	15	0.3	9
Oligochaeata	0.8	2	0	0
Arachnida	0.5	10	0	0
Odonata	0.5	8	2.1	12
Trichoptera	0.4	2	0	0
Copepoda	tr[e]	2	0	0
Total animal	68.3	98	52.5	79
Seeds[f]	31.7	65	43.6	76
Plant material	0	0	3.9	12
Total plant	31.7	65	47.5	79

[a] Includes (in addition to Chironomidae) Ceratopogonidae, Chaoboridae, Culicidae, and unidentified adults and larvae.
[b] Includes Lymnaeidae, Physidae, and Planorbidae.
[c] Includes Corixidae and Notonectidae.
[d] Includes Curculionidae, Dytiscidae, Haliplidae, and unidentified.
[e] Trace (<0.5% aggregate percent dry mass).
[f] Includes *Carex, Echinochloa, Eleocharis, Glyceria, Polygonum, Potamogeton, Scirpus,* and unidentified.

of females, and *Polygonum* (44%) and *Scirpus* (36%) seeds were the primary plant foods consumed by males.

DISCUSSION

Diet comparisons with prairie-nesting species.—Cinnamon Teal are similar to other dabbling ducks in that the female diet contains a greater proportion of invertebrates during breeding than during the nonbreeding period (Krapu and Reinecke 1992). Plant foods comprised 63–91% of the diet during fall migration in the Rio Grande Valley (Thorn and Zwank 1993) and 67% of the diet on Mexican wintering areas (Migoya and Baldassarre 1993). In contrast, animal foods comprised 68% of the diet of females in this study and 30–74% of the diet of spring migrant females in the Rio Grande Valley (Thorn and Zwank 1993). Cinnamon Teal are also similar to several other dabbling ducks in that invertebrate con-

sumption by breeding females was highest during laying (Krapu and Reinecke 1992).

Increased consumption of invertebrate foods by female Cinnamon Teal was probably related to protein demands associated with molt (Heitmeyer 1988) and with clutch production (Alisauskas and Ankney 1992). Females in all reproductive categories were engaged in prebasic molt (Gammonley, unpubl.; see also Thorn and Zwank 1993), and laying females also rely primarily upon exogenous sources to meet the large protein demands of clutch production (Gammonley, unpubl. data). The protein content of invertebrates is typically much higher than in most plant foods consumed by dabbling ducks (Krapu 1979). Thus, when invertebrate foods are readily available, molting and breeding female Cinnamon Teal likely meet their nutrient requirements more efficiently with an invertebrate-dominated diet.

Like many prairie-nesting *Anas* species, laying Cinnamon Teal use stored lipid reserves during clutch production (Gammonley, unpubl., Alisauskas and Ankney 1992). In contrast to large-bodied species such as the Mallard (*A. platyrhynchos*; Krapu 1981) that can acquire lipid reserves before arrival on breeding areas, female Cinnamon Teal obtain reserves after arrival in Arizona, prior to and during RFG (Gammonley, unpubl. data). By feeding >50% of diurnal hours, female Cinnamon Teal apparently obtain sufficient lipids to acquire reserves from a diet of invertebrates and seeds, despite the relatively low lipid content of these foods (Krapu 1979).

Although important invertebrate taxa (dipterans and gastropods) were similar, the invertebrate proportion of the diet of laying female Cinnamon Teal on high-elevation wetlands in Arizona was less than for prairie-nesting Blue-winged Teal (*A. discors*). Invertebrates comprised 99% (volume) and 90–94% (dry mass) of laying female Blue-winged Teal diets in North Dakota (Swanson et al. 1974a, Swanson and Meyer 1977) and Saskatchewan (Young 1991), respectively. These species are morphologically similar, and Blue-winged Teal also depend on exogenous food sources to meet protein requirements of egg formation (Young 1991). Few Blue-winged Teal breed in Arizona (Brown 1985), so direct comparisons of diets of these species on the study area were not possible. I did not measure invertebrate abundance quantitatively, but higher invertebrate availability on prairie wetlands compared to high-elevation wetlands in Arizona may contribute to diet differences between Cinnamon and Blue-winged teal (see below).

Sex-related differences in feeding ecology.—Comparisons of the feeding ecology of breeding Cinnamon Teal pairs support the hypotheses that pre-breeding and breeding females select animal foods and require more

food and feeding time than males. Differences between females and males in invertebrate proportion of the diet, mass of food contents, and time spent feeding can be attributed primarily to sex-related differences in nutritional requirements, because by comparing pair members collected while feeding together, I controlled any influences of time of day, season, weather, wetland habitat, and food item availability on selection of food resources (Krapu and Reinecke 1992). Laying female Gadwalls (*A. strepera*) also ate more invertebrates than did their mates (Serie and Swanson 1976) on prairie wetlands. Males do not molt before or during nesting (Gammonley, unpubl. data), and have a much lower energetic commitment to clutch formation than females (Alisauskas and Ankney 1992). Males do not use nutrient reserves from arrival through laying (Gammonley, unpubl. data) and apparently meet the energetic costs of vigilance and mate defense by feeding approximately 50% of diurnal hours.

Diet differences related to location.—Invertebrate foods, and particularly chironomids, comprised a higher proportion of foods consumed by female Cinnamon Teal on effluent marshes than on White Mountain wetlands. Chironomids dominated the invertebrate community at effluent marshes (Piest and Sowls 1985), whereas few chironomids were detected in a study of invertebrate communities on White Mountain wetlands (Buege 1993). My qualitative observations suggest that overall invertebrate abundance on Anderson Mesa wetlands is intermediate between effluent marshes and White Mountain wetlands. Differences in water quality (Stull and Kessler 1978, Piest and Sowls 1985), elevation and dominant vegetation among these three locations may influence invertebrate community characteristics (Reid 1985). Cinnamon Teal apparently forage on chironomids when they are available and abundant, as do many prairie-nesting ducks (Swanson and Meyer 1977, Woodin and Swanson 1989). On high-elevation natural wetlands in Arizona, Cinnamon Teal apparently meet the nutrient and energy requirements of breeding from a diet comprised of various invertebrate and seed taxa.

ACKNOWLEDGMENTS

W. D. Zeedyk (U.S. Forest Service, retired) was a key figure in stimulating research on southwestern high-elevation wetlands. He and M. E. Heitmeyer are largely responsible for generating funding for this research. This study was funded by the Institute for Wetland and Waterfowl Research of Ducks Unlimited, Inc. and the U.S. Forest Service, and it is a contribution from the Gaylord Memorial Laboratory (University of Missouri–Columbia and Missouri Department of Conservation cooperating) and the Missouri Agricultural Experiment Station, Journal Series No. 12,058. C. Hinshaw, B. Jones, T. Perren, and J. Windes assisted in collecting time-activity data. D. R. Patton of Northern Arizona University kindly provided access to laboratory space and equipment. B. D. Dugger, L. H. Fredrickson, and P. A. Magee provided helpful reviews of an earlier draft of the manuscript.

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Wilson Bull., 107(1), 1995, pp. 73–80

PREDATOR-PREY RELATIONSHIP BETWEEN WILSON'S PLOVERS AND FIDDLER CRABS IN NORTHEASTERN VENEZUELA

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ABSTRACT.—In coastal lagoons of northeastern Venezuela, resident Wilson's Plovers (*Charadrius wilsonia cinnamominus*) forage almost entirely on fiddler crabs (*Uca cumulanta*). During the non-breeding season, particularly from November to January, plovers are seldom on foraging sites during daylight but forage more during nighttime. Objectives of this study were to document the availability of *Uca cumulanta* and to determine if night foraging by Wilson's Plovers in tropical areas is tied to abundance or activity of fiddler crabs. We used a time-lapse video camera to monitor the number of crabs outside burrows, both during nighttime and daytime. Results show that crab activity was almost exclusively diurnal. Although some crabs were active after sunset, particularly from May to August, diurnal activity of crabs was always 3–10× higher than nocturnal activity. Therefore, Wilson's Plovers feeding patterns are not exclusively a function of the period when their main prey is most active or abundant. Results best support our previous interpretation that nocturnal foraging in Wilson's Plover is a strategy for avoiding diurnal predators. *Received 17 May 1994, accepted 15 Sept. 1994.*

Recent studies on shorebirds in northeastern Venezuela and Mauritania have shown that Holarctic winter migrants and Neotropical resident species regularly feed at night in tropical environments (Robert et al. 1989, Zwarts et al. 1990, McNeil et al. 1992). There are two main hypotheses to explain why shorebirds forage at night: (1) the "supplementary hypothesis" which postulates that night feeding occurs when daytime feeding has been inadequate to meet the birds' energy requirements and (2) the "preference hypothesis" which postulates that the birds prefer to feed at night because it provides the most profitable, or the safest, feeding opportunities (see review by McNeil 1991, McNeil et al. 1992). Direct observations indicate that at night invertebrate prey items are more active or closer to the sediment surface where shorebirds forage (see McNeil et al. 1992). Similarly, the abundance of swimming prey such as fishes and insects appears to be higher at night than during daylight (Robert and McNeil 1989, McNeil and Robert 1992). In some species, individuals apparently forage at night to take advantage of nocturnally active prey and/or to avoid diurnal predation, only feeding in daytime to supplement a nighttime deficit in energy intake (see Batty 1991, McNeil et al. 1992).

In coastal lagoons of northeastern Venezuela, the resident race of the Wilson's Plover (*Charadrius wilsonia cinnamominus*) forages mainly

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(98% of their diet) on the fiddler crab *Uca cumulanta,* as do Willets (*Catoptrophorus semipalmatus*) and Whimbrels (*Numenius phaeopus*) (Morrier and McNeil 1991, McNeil and Rompré 1995). Crabs occupy the intertidal zones year-round. During their non-breeding season, particularly from November to January, the plovers' presence on foraging sites is very short during daylight but is counterbalanced by an increase during nighttime (Thibault and McNeil 1994). Day and night distributions of plovers over lagoon habitats differ substantially. Wilson's Plovers are gregarious and spend most of their time roosting during the day. After dusk, they leave their diurnal roosts and distribute themselves solitarily throughout the lagoon mudflats or fly to nocturnal individual roosts close to mangroves (Thibault and McNeil 1994). They forage during low tides, but never during the entire low-tide period, neither during daytime nor during nighttime. They also spend more time on foraging sites during the first part of the night (19:00–22:00 h) than thereafter. Morrier and McNeil (1991) and Thibault and McNeil (1994) suggested that the main reason why Wilson's Plovers are largely nocturnal is to avoid diurnal predators.

Most *Uca* species are predominantly diurnal (Young and Ambrose 1978, Zucker 1978, Zwarts 1990), but some species are active after sunset, e.g., *U. tangeri* in Mauritania (Zwarts 1990). Predator-prey relationships between shorebirds and fiddler crabs have been investigated mainly by Zwarts (1990) and Zwarts and Dirksen (1990) who considered the dependency of Whimbrels on *U. tangeri* for foraging after sunset when wintering in Mauritania.

Due to the large dependency of Wilson's Plovers on fiddler crabs and their peculiar habit of being active on foraging sites almost exclusively at night during the non-breeding season, the objectives of this study were (1) to document the monthly and diel availability of *U. cumulanta* in coastal Venezuela and (2) to determine whether night foraging in Wilson's Plovers in tropical areas is tied to the nocturnal abundance and/or activity of fiddler crabs. The factors responsible for rhythms of activity and/or abundance of fiddler crabs are not considered in this paper.

STUDY AREA AND METHODS

The study was conducted around the Bocaripo lagoon, part of the Chacopata lagoon complex (10°40′N; 63°48′W) on the north side of the Araya Peninsula, State of Sucre, Venezuela, from January to August 1992. In that region, daytime is roughly 2-h longer in June than in December. Wilson's Plovers and their prey, *U. cumulanta,* are present in the complex year-round (Limoges 1987). We used a time-lapse video camera (Fieldcam WCMS type 6/V801 field television system assembled by Fuhrman Diversified Inc., LaPorte, Texas 77571) to monitor the number of crabs outside their burrows at 10-sec intervals in a 1 × 1 m area. Infrared lamps were used to avoid disturbing crab behavior during nighttime (i.e., between sunset and sunrise). These lamps produced no heat on the plot. More than 530 h

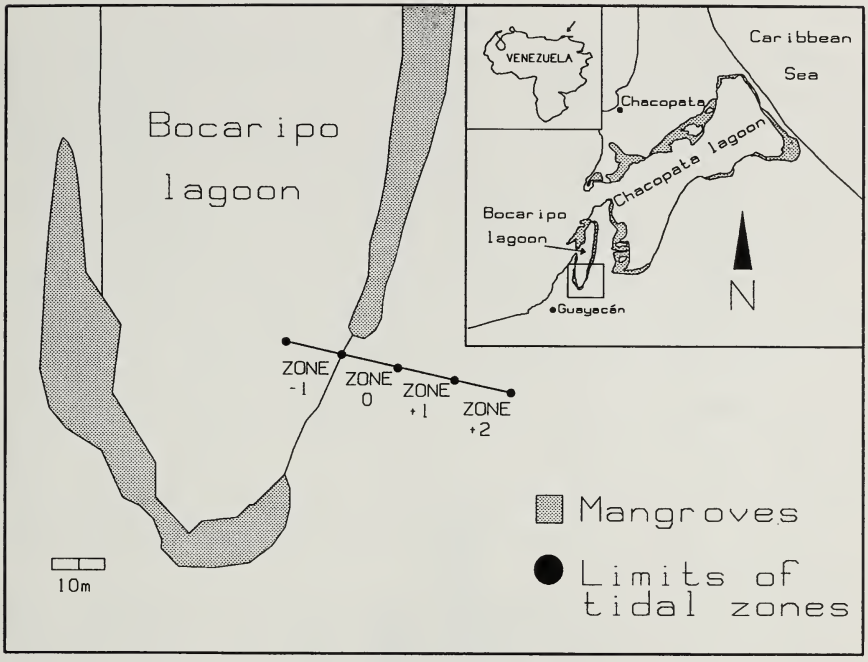

FIG. 1. Location of the transect for counting crab burrows on the shore of the Bocaripo Lagoon, State of Sucre, Venezuela.

were devoted to recording on six sites in turn around Bocaripo lagoon. The total recording time was distributed, as far as possible, equally from month-to-month during 24-h periods from March to July. In January, recording was done during only one 24-h period and, in February and August, data were collected only over one and two nights, respectively, with no recording during the daytime. At the same time that video-recording was being done, Wilson's Plovers feeding during nighttime in the surroundings of the video camera were counted hourly with a 6.8× nightscope (light intensification: ×60,000), model MK-303A (Star-tron Technology Corporation, Pittsburgh, Pennsylvania 15238, USA). In addition, from March to July 1992, we counted crab burrows in five 1 × 1 m plots distributed along a 48-m transect oriented perpendicularly to the tide line. The transect covered the entire intertidal zone (Fig. 1) from the upper tidal zone (zone +2) to the mud inside the lagoon (zone −1).

One-way ANOVA (Sokal and Rohlf 1981) was used to compare crab densities as a function of tide zones and to test the significance of hourly and monthly variation in fiddler crab activity (i.e., number of individuals outside burrows). Bartlett's test (Sokal and Rohlf 1981) was used to evaluate the homogeneity of variance on each data set before using ANOVA. In case of heterogeneity of variance, the nonparametric Kruskal-Wallis test was used (Sokal and Rohlf 1981). *G*-tests for goodness of fit to a uniform distribution (Sokal and Rohlf 1981) were performed to test the significance of hourly variation in crab activity for January (only one 24-h period). Finally, we employed Pearson's correlation coefficient to study the relationship between fiddler crab activity and plover night feeding activity.

RESULTS

Wilson's Plovers frequently were observed feeding on *Uca* crabs, both during daytime and nighttime. Wilson's Plovers are visual feeders and catch fiddler crabs by running after them. Very often, during daylight, when plovers came within a certain distance, fiddler crabs retreated underground into their burrows, preventing plovers from catching them. During nighttime, Wilson's Plovers were also observed catching some small prey, apparently insects, which abound on the mudflat at night.

From January through August, there was significant variation in crab numbers outside burrows. In May, June, and August, the nighttime crab density was significantly higher than during the January–April interval ($F_{1,82} = 30.89$, $P < 0.001$). It was also higher in July, compared to May, June and August ($H = 6.65$, df = 1, $P < 0.001$). Overall, from January through July, the presence of Wilson's Plovers feeding at night varied inversely with crab activity ($r = -0.735$, N = 7, $P < 0.05$; Fig. 2A). During daytime, monthly variation in crab numbers was significant ($F_{5,66} = 27.20$, $P < 0.001$), increasing from January through May and decreasing thereafter (Fig. 2B).

Each month, except February and August (no data for daytime), crabs were outside burrows in significantly higher numbers by day than by night (January: $G = 121.90$, df = 23, $P < 0.001$; March: $F_{19,72} = 11.30$, $P < 0.001$; April: $F_{20,94} = 5.39$, $P < 0.001$; May: $F_{21,34} = 5.16$, $P < 0.001$; June: $F_{23,75} = 10.31$, $P < 0.001$; and July: $F_{23,76} = 1.88$, $P < 0.05$; see Fig. 3). Overall, crab activity tended to be higher just after sunrise, except in April, due to high tide which took place during early morning. Although some activity was observed after sunset, particularly from May to August, the diurnal activity of crabs was always 3–10× higher than their nocturnal activity (Figs. 2 and 3).

Wilson's Plovers were seen feeding in zone 0 and, occasionally, in zone +1 of our transect (Fig. 1). During April and May, the mudflat dried up in zones +1 and +2. In fact, April and May had the lowest tides of the year. Nevertheless, the number of burrows in zones +1 and +2 did not vary during the five months ($F = 4.48$, ns; see Fig. 4). However, mainly due to May data, zone 0 was the one where the number of burrows reached the highest density ($F_{3,16} = 6.44$, $P < 0.01$). Since low tides began in March, the mudflats of zone −1 remained uncovered most of the time, and crabs used that zone more than before. But during other months, the water line remained in zone 0, and zone −1 was covered most of the time. As a consequence, fiddler crabs left this zone.

DISCUSSION

The time-lapse video camera revealed that each burrow was normally occupied by a crab. This indicates that the method used by Zwarts (1985),

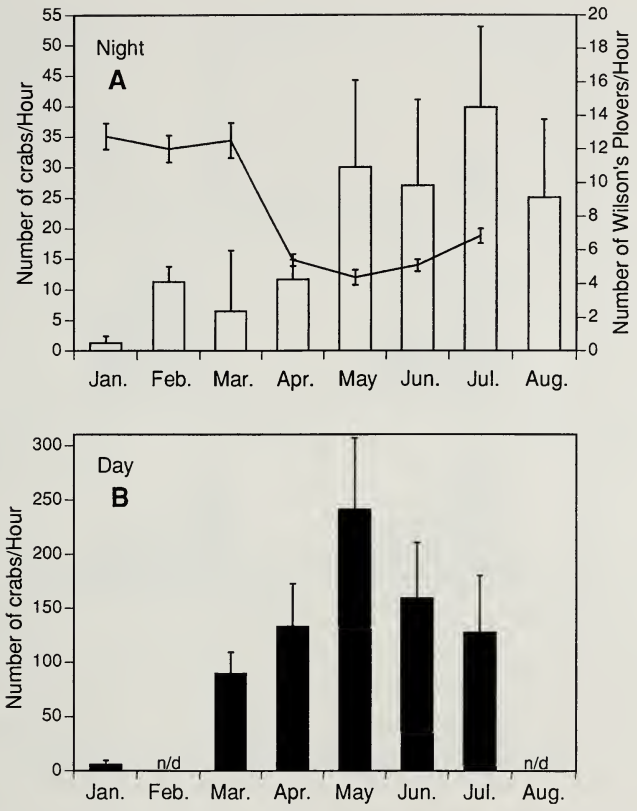

FIG. 2. Seasonal variation in the number of fiddler crabs observed per hour outside burrows (bars) during nighttime (A) and daytime (B). The line in A represents the variation in the number of Wilson's Plovers foraging at night. Vertical lines represent 95% confidence intervals and n/d indicates the absence of data.

i.e., count of burrows, is appropriate to estimate crab density. Our count of burrows revealed that zone 0 of our transect (Fig. 1) had the highest crab density. This zone also supported the majority of Wilson's Plovers feeding on the mudflat.

Zwarts (1990) reported that *U. tangeri* is active during the first part of the night in Mauritania. In Chacopata, *U. cumulanta* remained active after sunset, but their activity was always three to 10 times lower at night than during the day (Figs. 2 and 3). In addition, they showed no preference for any particular part of the night, their activity being low but regular from dusk to dawn, particularly from May to August (Figs. 2 and 3). Taking into account the fact that *U. cumulanta* is considerably less active at night than during the day, the fact that Wilson's Plovers, during the

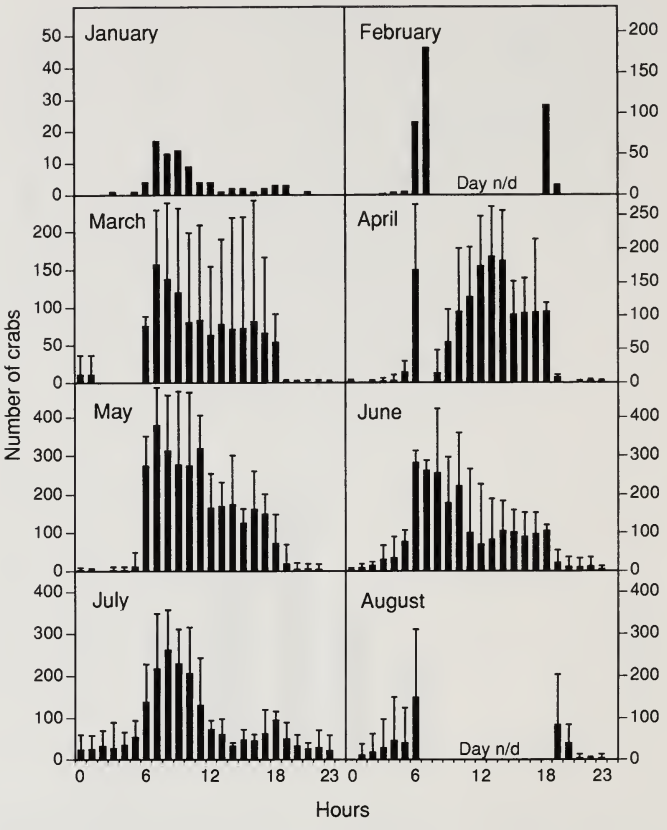

FIG. 3. Diel variation in the number of fiddler crabs recorded outside burrows between January and August. Vertical lines represent 95% confidence intervals and n/d indicates the absence of data.

non-breeding season, rest during daytime and forage almost exclusively during the nighttime cannot be interpreted as a strategy to take advantage of the period when their main prey is most active and/or abundant. This conclusion is reinforced by the fact that, overall, the presence of Wilson's Plovers feeding at night varied inversely with nocturnal crab activity. Morrier and McNeil (1991) suggested that nocturnal foraging by Wilson's Plovers is a strategy for avoiding diurnal aerial predators. This study supports that explanation. In fact, why should the plovers complicate their life by avoiding foraging when their prey are more plentiful and can more easily be detected by sight? Nevertheless, the activity of *Uca* crabs, although much lower at night than during daytime, appeared sufficient for Wilson's Plovers to forage almost exclusively during nighttime.

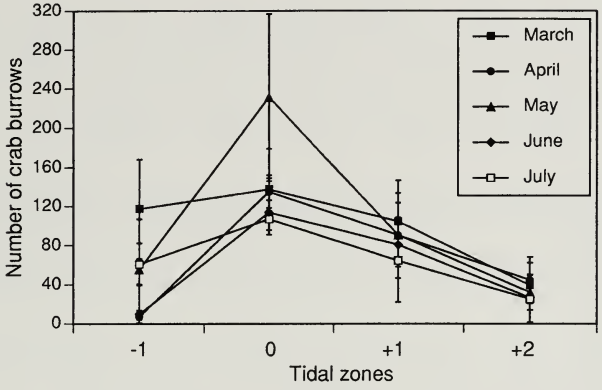

FIG. 4. Monthly variation in the number of burrows of fiddler crabs counted per m^2 as a function of tidal zones for each month between March and July. Vertical lines represent 95% confidence intervals.

The number of *Uca* crabs per hour outside burrows (Fig. 2B) was highest in May, and the extent of their nighttime activity started increasing in May and was at a maximum in July (Fig. 2A). In the Chacopata Lagoon complex, Wilson's Plovers start egg-laying at the beginning of May and the last eggs hatch around mid-August (Thibault 1993, Thibault and McNeil, unpubl. data). In accordance with the hypothesis that breeding seasons of birds have evolved so that the birds have their young when food is most available (see Lack 1954, Marshall 1961), we suspect that Wilson's Plovers start breeding when food resources become more abundant and, particularly, in such a way that hatching coincides with the time when nocturnal abundance of *Uca* crabs outside burrows is highest, thus ensuring better feeding success for chicks. In addition, during the laying and incubation periods, compared with the non-breeding season, the feeding pattern of Wilson's Plovers changes radically; during nighttime, males incubate most of the time and females forage (Thibault 1993, Thibault and McNeil, unpubl. data). Males and non-breeding individuals forage during the daytime (Thibault 1993); this could explain the decrease in the number of plovers observed feeding at night during April as compared with January–March.

ACKNOWLEDGMENTS

This study was supported by the Natural Sciences and Engineering Research Council of Canada and the Univ. de Montréal. We thank G. Rompré for help during the field work. We are also indebted to colleagues of the Univ. de Oriente, and in particular, J. R. Rodríguez S., who is co-responsible with R. McNeil for the collaboration agreement between that university in Venezuela and the Univ. de Montréal.

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Wilson Bull., 107(1), 1995, pp. 81–92

LOSSES OF RED-COCKADED WOODPECKER CAVITY TREES TO SOUTHERN PINE BEETLES

Richard N. Conner and D. Craig Rudolph[1]

Abstract.—Over an 11–year period (1983–1993), we examined the southern pine beetle (*Dendroctonus frontalis*) infestation rate of single Red-cockaded Woodpecker (*Picoides borealis*) cavity trees on the Angelina National Forest in Texas. Southern pine beetles infested and killed 38 cavity trees during this period. Typically, within each cavity tree cluster, beetles infested only a single tree (usually the nest tree of the previous spring) during autumn and used the cavity tree as an over-wintering site for brood development. Seven (4 active and 3 inactive) cavity trees (out of 346 cavity tree years) died as a result of beetle infestation during the first five years of the study (1983–1987). In 1988, an intensive habitat management program was initiated on the forest to halt a severe population decline of the woodpecker. During the next six years (1988–1993), a much higher mortality rate was observed; 31 single cavity trees (out of 486 cavity tree years) were infested and killed ($\chi^2 = 8.8$, $P < 0.003$). Southern pine beetle-caused mortality of cavity trees also was high on other Texas national and state forests during this period. This marked increase of beetle-caused cavity tree mortality during a period of increased intensity of necessary management is of extreme concern. As a result of high beetle-caused mortality of active cavity trees, 64% of active cavity trees being used by Red-cockaded Woodpeckers on the northern portion of the Angelina National Forest during 1993 were artificial cavities. Pines selected by biologists for cavity inserts may produce less resin than those selected by woodpeckers and not provide an adequate barrier against snakes. The relationship between infestation of single active cavity trees and the number of beetle infestations (spots) on the northern portion of the Angelina National Forest from 1984 to 1993 was inconclusive ($r = 0.56$, $P > 0.09$, $N = 10$); further research is needed for a definitive conclusion. *Received 13 Apr. 1994, accepted 14 Sept. 1994.*

In the southeastern United States, old pines required for Red-cockaded Woodpecker (*Picoides borealis*) cavity excavation (Conner and O'Halloran 1987, Rudolph and Conner 1991) are rare, and the current age structure of pines on most national forests indicates that this shortage is likely to continue for at least 20 years (Conner and Rudolph 1989, Costa and Escano 1989). Provision of adequate old growth pines as potential cavity sites for this endangered woodpecker is a key element for its recovery.

Southern pine beetles (*Dendroctonus frontalis*) are the major cause of cavity tree death on Texas national forests (Conner et al. 1991). Growth of multiple-tree infestations (beetle spots) normally occurs from early spring to late summer (Coulson et al. 1972, Belanger et al. 1993), is facilitated by attractant pheromones (Thatcher et al. 1980), and can rap-

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idly eliminate entire cavity tree clusters. More than 350 cavity trees, which included more than 50 entire cavity tree clusters, were killed by southern pine beetles during a major infestation in the Four-Notch area of the Sam Houston National Forest between 1983 to 1985 (Billings and Varner 1986, Conner et al. 1991).

Although less catastrophic, annual losses of single cavity trees to southern pine beetle infestations appear to be persistent and cumulative. Bark beetle infestation of single cavity trees primarily affects active woodpecker cavity trees. Such trees are typically infested during the fall and serve as over-wintering sites for beetle brood development, with southern pine beetles emerging prior to summer of the following year (Conner et al. 1991, Rudolph and Conner 1995). Regular annual losses of cavity trees by single tree infestations have the potential to impact woodpecker groups significantly over the long term by limiting sufficient numbers of cavities for roosting and nesting. Cavity excavation by woodpeckers for replacement of dead cavity trees can require from one to four years ($\bar{x}$ = 2.4 years for shortleaf pine and 1.8 years for loblolly pines, Conner and Rudolph 1995).

Southern pine beetle infestation is not normally a problem in longleaf pines (*Pinus palustris*) because of this species' copious production of pine resin which serves as the pine's first line of defense against beetle infestation (Wahlenberg 1946, Hodges et al. 1977). Loblolly (*P. taeda*) and shortleaf (*P. echinata*) pines produce less resin, and generally are more susceptible to southern pine beetle infestation.

Following reports of severe woodpecker population declines (Conner and Rudolph 1989, Costa and Escano 1989) and a 1988 federal court case (Bigony 1991, MacFarlane 1992), the National Forest System intensified cluster area management on National Forests in Texas, and on nearly all other national forests in the south between 1988 and 1993, in an urgently needed effort to reverse the severe population declines. This intensified management included complete removal of hardwood tree species and substantial reduction of pine basal area to bring clusters into the 14 to 16 m^2/ha basal area range ordered by the federal court. Typically, the entire hardwood and pine midstory was removed by mechanical equipment (Conner and Rudolph 1991). Starting in 1990, an aggressive program was initiated to install artificially drilled cavities and cavity inserts using the techniques of Copeyon (1990) and Allen (1991) to give woodpecker groups sufficient cavities for nesting and roosting. As a response to events on national forests, management efforts for Red-cockaded Woodpeckers also were intensified on the W. Goodrich Jones and I. D. Fairchild State Forests in Texas during the late 1980s.

In this paper, we examine past baseline and recent increases in beetle

caused mortality on the northern portion of the Angelina National Forest, which is primarily a loblolly-shortleaf pine forest. Southern pine beetle infestations of single cavity trees on the Sam Houston and Davy Crockett National Forests and two state forests in Texas also are examined. We explore the hypothesis that southern pine beetle caused mortality of Red-cockaded Woodpecker cavity trees on the Angelina National Forest is a function of ambient beetle population levels in the surrounding forest habitat.

STUDY AREAS AND METHODS

The Angelina National Forest (62,423 ha; 31°15′N, 94°15′W) is located in eastern Texas. The northern portion of the Angelina National Forest is predominantly covered by loblolly and shortleaf pines, whereas longleaf pine is the dominant tree species on the southern portion of the forest in the areas where Red-cockaded Woodpeckers are found (Conner and Rudolph 1989). The Davy Crockett (65,329 ha; 31°21′N, 95°07′W) and Sam Houston (65,218 ha; 30°30′N, 95°22′W) National Forests are both predominantly loblolly and shortleaf pine. The I. D. Fairchild (648 ha; 31°47′N, 95°22′W) and W. Goodrich Jones (688 ha; 30°13′N, 95°29′W) State Forests are primarily shortleaf and loblolly pine.

The loblolly-shortleaf pine habitat where Red-cockaded Woodpecker clusters are located occurs mainly on mesic, shrink-swell clays (Woodtel and LaCerda soil types), which readily support growth of hardwood vegetation (Fuchs 1980). Varying moisture conditions throughout the year produce the shrink-swell characteristics of the soils, which can strip root hairs off lateral roots of both pines and hardwood vegetation. Such soils place considerable stress on the plant communities they support and can increase the hazard of southern pine beetle infestation (Lorio et al. 1982, Mitchell et al. 1991). Longleaf pines occur primarily on deep loamy sands (Tehran and Letney soil types) containing materials of volcanic origin (Neitsch 1982). These soils contain very little organic material, resulting in a low water holding capacity. High soil temperatures during summer and limited water in these soils limit the growth of hardwoods on these sites but do not negatively affect longleaf pine resin production. Historically, southern pine beetle infestation of cavity trees in the longleaf pine habitats of the Angelina National Forest has been minimal (Conner et al. 1991).

The woodpecker population on the Angelina National Forest is comprised of widely separated isolated subpopulations (Conner and Rudolph 1989). Woodpeckers on the northern side of the Angelina National Forest (12 active clusters) are 34 km (including the 4–6 km wide Sam Rayburn reservoir) from 15 active clusters in the two southern subpopulations.

We made annual spring visits to all Red-cockaded Woodpecker cavity trees on the Angelina National Forest in eastern Texas (1983 through 1993) to evaluate cavity tree status and condition, using the indicators described by Jackson (1977, 1978). Active cavity tree clusters were visited several times per year. We examined each cavity tree to ascertain activity at resin wells (number of active wells and a subjective estimate of volume of resin flowing from the wounds), amount of scaling of bark, and condition of the cavity entrance. We determined the occurrence and causes of cavity tree mortality (Conner et al. 1991). Cavity trees infested by southern pine beetles typically had numerous white "popcorn-like" pitch tubes of crystallized pine resin around wounds where individual beetles had chewed through the bark and into the cambium of the bole. Dead cavity trees with signs of bark beetle infestation were examined to determine whether lightning strikes were also associated with tree deaths. Records of southern pine beetle infestation of Red-cockaded Woodpecker cavity trees and cavity tree activity status on the Davy Crockett and Sam Houston National

Forests and the I. D. Fairchild and W. Goodrich Jones State Forests were obtained from respective forest biologists.

In order to compare ambient southern pine beetle population levels with annual losses of cavity trees, we obtained records of the annual number of southern pine beetle infestations (beetle spots) and the number of pines infested on the northern portion of the Angelina National Forest from the USDA Forest Service Pest Management Office in Pineville, Louisiana, and Atlanta, Georgia (SPBIS—Southern Pine Beetle Information System data base). The National Forest and Grasslands in Texas provided data on areas affected by midstory removal within Red-cockaded Woodpecker clusters between 1988 and 1993.

RESULTS

Southern pine beetles infested and killed 38 single Red-cockaded Woodpecker cavity trees (active and inactive combined) on the northern portion of the Angelina National Forest from fall 1983 through spring 1993. The number of woodpecker groups on the northern portion of the Angelina National Forest ranged between seven and 10 over this 11 year time span. Southern pine beetles typically infested cavity trees during the fall (October and November), and trees appeared dead (dropped all needles and some bark pecked off by woodpeckers at mid bole height) by the following spring (March through June). Seven cavity trees (out of 346 cavity tree years) were killed by single-tree beetle infestation during the five-year period (1983–1987) immediately prior to initiation of intensive management for Red-cockaded Woodpeckers (Table 1). During the next six years, when intensive management occurred (1988–1993, Table 2), 31 cavity trees (out of 486 cavity tree years) were killed. This was a much higher mortality rate (6.3% vs 2.0%) than during the previous five-year period ($\chi^2 = 8.8$, $P = 0.003$). Seven of these 31 cavity trees were killed between fall 1991 and spring 1992 and 14 during the same time period the following year (Fig. 1).

Active cavity trees on three national and two state forests (Table 1) were infested at a higher average annual rate per year ($\bar{x} = 10.9 \pm 10.7\%$) than inactive trees ($\bar{x} = 0.8 \pm 1.3\%$, $t = 4.31$, $P = 0.0003$) (also see Rudolph and Conner 1995). This was particularly apparent during the 1988–1992 five-year period on the Angelina National Forest (Fig. 2). The majority of cavity tree mortality on the Angelina National Forest occurred within active cavity tree clusters (Fig. 3).

Fifty-five percent (21 of 38) of the beetle-caused cavity tree mortality occurred during the last two years of the 11-year period ($\chi^2 = 38.7$, $P < 0.001$). Thirty-three and 44 active cavity trees were present on the northern portion of the Angelina National Forest during 1991–1992 and 1992–1993, respectively. Thus, the loss of seven active cavity trees in 1991–1992 represents a 21% loss of active cavity trees, and the 14 active cavity trees killed in 1992–1993 represents a 32% loss (Table 1). Rates of single

TABLE 1

SOUTHERN PINE BEETLE INDUCED MORTALITY OF LOBLOLLY AND SHORTLEAF PINE, RED-COCKADED WOODPECKER CAVITY TREES ON NATIONAL AND STATE FORESTS IN EASTERN TEXAS

Forest	Year	No. active cavity trees	No. inactive cavity trees	Active SPB killed		Inactive SPB killed	
				N	%	N	%
Angelina N. F.	1993	44	63	14	32	0	0
	1992	33	39	7	21	0	0
	1991	33	44	0	0	1	2
	1990	29	44	2	7	0	0
	1989	34	45	3	9	1	2
	1988	29	49	3	10	0	0
	1987	28	46	0	0	2	4
	1986	28	44	1	4	0	0
	1985	27	44	2	7	0	0
	1984	46	24	0	0	1	4
	1983	34	25	1	3	0	0
Davy Crockett N. F.	1993	192	429	11	6	8	2
	1992	184	405	24	13	4	<1
	1991	117	406	4	3	2	<1
	1990	90	372	5	6	2	<1
Sam Houston N. F.	1993	438	1303	35	8	7	<1
	1992	425	1184	29	7	10	<1
I. D. Fairchild State Forest	1993	16	48	6	38	0	0
	1992	17	45	5	29	0	0
Jones State Forest	1993	40	73	4	10	0	0
	1992	36	70	6	17	1	1

TABLE 2

AREA WITH MIDSTORY REMOVAL COMPLETED WITHIN RED-COCKADED WOODPECKER CLUSTERS ON NATIONAL FORESTS IN TEXAS BETWEEN 1988 AND 1993

	Year of management activity				
	1988–1989	1989–1990	1990–1991	1991–1992	1992–1993
Midstory removal (ha)					
Angelina N. F.	0	127	170	102	75
Davy Crockett N. F.	273	163	90	153	101
Sam Houston N. F.	139	174	1023	331	86
Total	598	522	1444	796	314

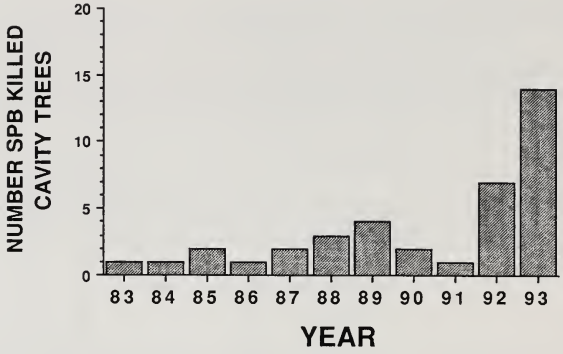

FIG. 1. Number of single Red-cockaded Woodpecker cavity trees infested and killed by southern pine beetles on the northern side of the Angelina National Forest before (1983–1987) and after (1988–1992) intensive woodpecker management was initiated.

cavity tree losses to southern pine beetles also were high on state forests; during 1991–1992 and 1992–1993 a total of 11 and 10 active cavity trees, respectively, were killed by southern pine beetles on the W. Goodrich Jones and I. D. Fairchild State Forests. The highest loss rates of any forest (29% and 38%) were observed on the I. D. Fairchild State Forest (Table 1). Although not as high as loss rates on the Angelina National Forest, losses on the Davy Crockett and Sam Houston National Forests during 1991–1992 and 1992–1993 were substantial (Table 1).

On the northern portion of the Angelina National Forest the number of detected southern pine beetle infestations (spots) and the number of pines infested within these spots varied considerably from 1984 through 1993 (Fig. 4A, B). The annual number of single cavity trees infested by

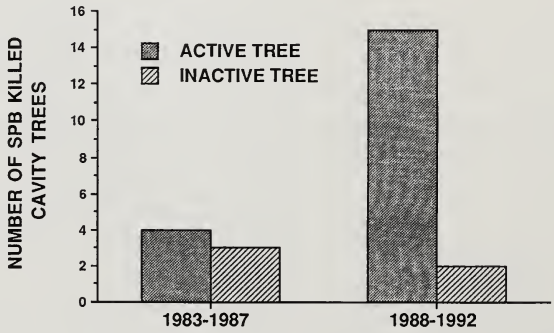

FIG. 2. Number of active and inactive Red-cockaded Woodpecker cavity trees killed by southern pine beetles before (1983–1987) and after (1988–1992) intensive woodpecker management was initiated on the Angelina National Forest.

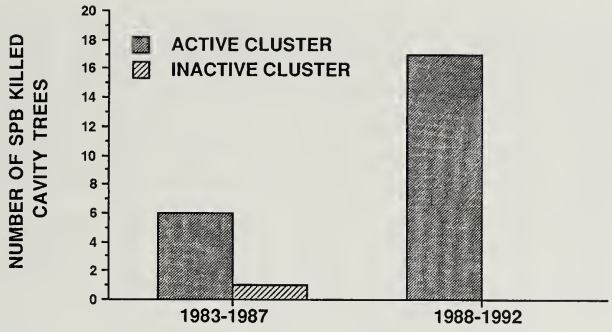

FIG. 3. Number of Red-cockaded Woodpecker cavity trees killed by southern pine beetles within active and inactive clusters during 1983–1987 and 1988–1992 on the Angelina National Forest.

southern pine beetles was marginally correlated with the number of southern pine beetle infestations ($r = 0.56$, N = 10, $P = 0.09$) but not correlated with the total number of pines infested within the general area ($r = 0.27$, $P = 0.44$) of the cavity tree clusters. However, the sample sizes for these correlations were small, and thus the biological significance of the results remains inconclusive.

DISCUSSION

The increase in southern pine beetle-caused mortality of Red-cockaded Woodpecker cavity trees beginning in 1988 is of extreme concern. The coincidental timing of increased cavity tree losses with initiation of intensive management suggests that efforts to correct habitat problems may be associated with increases in southern pine beetle infestation of active cavity trees. Physical disturbance of soils and root systems of trees during thinning and midstory removal operations is known to increase the risk of beetle infestation and the susceptibility of pines to attack (Nebeker and Hodges 1985, Hicks et al. 1987, Mitchell et al. 1991). Infestation of cavity trees occurred primarily within active woodpecker clusters. Intensive management activities were focused primarily on active cavity tree clusters when they were first initiated, again suggesting the possibility of a relationship between cluster management activities and beetle infestation of cavity trees. The most aggressive midstory and thinning work was completed between 1989 and 1991 on the Angelina National Forest; but the mortality rates of cavity trees were highest during 1992 and 1993 when southern pine beetle populations were at high levels. Midstory removal and thinning of pines was restricted to woodpecker cluster areas and did not include the surrounding general forest. Thus, present man-

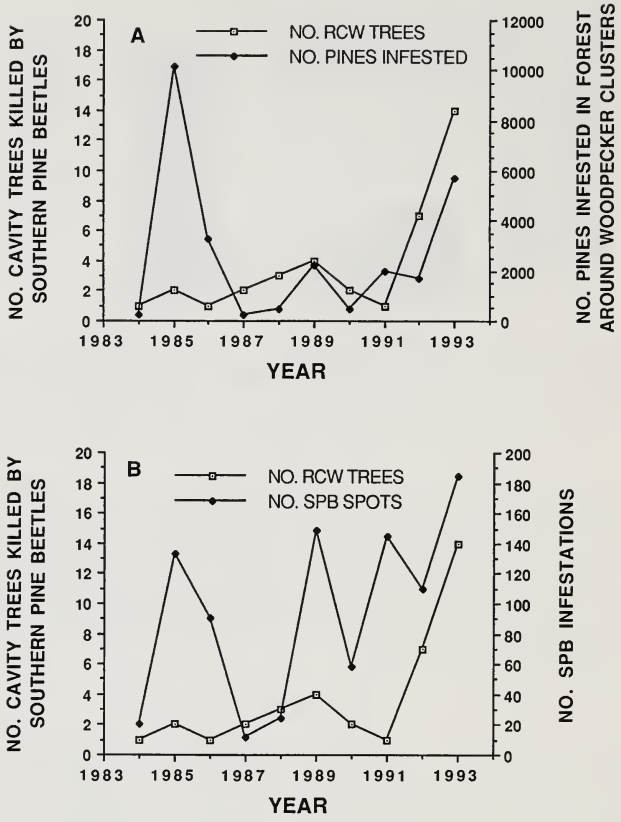

FIG. 4. Number of single Red-cockaded Woodpecker cavity trees killed by southern pine beetles versus the number of pines infested by southern pine beetles (A) and the number of southern pine beetle infestations (B) on the northern portion of the Angelina National Forest from 1983 through 1993.

agement produces a pocket of relatively open pine forest surrounded by a sea of pines and dense hardwood midstory. Southern pine beetles have a search image for vertically oriented dark objects—e.g., pine boles, and hardwood foliage is known to interfere with beetle movements (Showalter and Turchin 1993). Green leaf volatiles from deciduous foliage also interrupt bark beetle aggregation response to attractant pheromones when infesting southern pines (Dickens et al. 1992). Management's creation of islands of open pine forest within a sea of forest with midstory may serve as "magnets" to increase southern pine beetle numbers within Red-cockaded Woodpecker cluster areas.

In addition, woodpecker pecking at resin wells may elevate suscepti-

bility of cavity trees to infestation either by decreasing tree vigor or by creating a wick of resin volatiles that serves as an attractant for southern pine beetles. When Red-cockaded Woodpeckers initially excavate resin wells in a pine around a newly completed cavity, resin flow from the wound is typically high because the pine actively transports oleoresins to the wound site (Ross et al. 1991, 1993). As woodpecker excavation of resin wells continues through time, resin flow to excavated wells in loblolly and shortleaf pine often decreases, perhaps to levels below what is adequate for defense against southern pine beetles (Ross et al. 1993). This would account for the fact that active cavity trees were infested at a higher rate than inactive trees (Table 1).

Resin flow to wound sites serves as the pine's primary defense against infesting southern pine beetles (Schmitt et al. 1988), but it is influenced by periods of active tree growth, moisture, temperature, and season of the year (Lorio 1986). Trees infested by southern pine beetles during the fall are often those that have been recently hit by lightning and serve as overwintering sites for beetle brood development (Coulson et al. 1983, Blanche et al. 1985). Lightning strikes impair the pine's ability to transport oleoresins (Blanche et al. 1985), perhaps similar to decreased resin flow resulting from continued Red-cockaded Woodpecker excavation of resin wells in loblolly and shortleaf pines. There are similarities between lightning-struck pines and loblolly and shortleaf pine cavity trees that may increase their susceptibility to successful infestation by southern pine beetles.

Fortunately, the severe losses of cavity trees to southern pine beetle infestation can be offset by the new technology of artificial cavity installation (Copeyon 1990, Allen 1991). As cavity trees are killed by southern pine beetles, new cavity inserts are installed to replace the lost trees. Over 100 cavity inserts were installed on the Angelina National Forest during 1992 alone (pers. commun., Alfredo Sanchez, District Biologist, Angelina National Forest). As a result of the cavity tree mortality and the insert program to offset it, 28 of 44 (64%) active cavity trees being used by Red-cockaded Woodpeckers on the northern Angelina National Forest during 1993 had artificial cavities. This percentage is likely to increase as beetles kill more natural cavity trees and more cavity inserts are installed. However, pines with artificial cavities are also susceptible to southern pine beetle infestation, particularly when Red-cockaded Woodpeckers begin to use them. Ninety-three percent (13 of 14) of cavity trees killed by southern pine beetles between fall 1992 and spring 1993 contained artificial cavities.

Southern pine beetle populations in the general forest area around woodpecker cavity tree clusters would likely have an influence on infes-

tation of cavity trees. However, on the northern portion of the Angelina National Forest, we failed to detect a significant relationship between infestation of single Red-cockaded Woodpecker cavity trees and measures of the ambient southern pine beetle population. Our sample size was quite low (N = 10), which limited statistical power. The lack of a clear relationship between ambient beetle populations and cavity tree mortality suggests that factors such as management of cluster areas or individual cavity tree characteristics (pine tree volatiles in resins) may be associated with the infestation of single Red-cockaded Woodpecker cavity trees.

Long-term effects of woodpecker use of primarily artificial cavities are unknown. When excavating natural cavities, woodpeckers may select pines that produce desired amounts of pine resin (Conner and O'Halloran 1987). Pines selected by biologists for cavity installation may have different resin characteristics than those selected by woodpeckers. If such pines are unable to produce sufficient resin to repel southern pine beetles, they also may not be able to produce enough resin at resin wells for barriers to adequately protect cavity trees from climbing rat snakes (*Elaphe obsoleta*) (Rudolph et al. 1990).

Additional research is needed to explore relationships among woodpecker management, southern pine beetle infestation of single cavity trees, and ambient beetle population levels. Information is needed to determine if woodpecker cluster area management accumulates beetles around cavity trees by creating open patches of mature pines within otherwise dense vegetation. Although there is experimental evidence that southern pine beetles are not attracted to certain host volatiles (alpha pinene) (Billings 1985, Thatcher et al. 1980), production of all host volatiles at resin wells also needs examination as a possible attractant for southern pine beetles.

Southern pine beetles are a problem pest in southern pines throughout the southeastern United States (Thatcher et al. 1980). Verbal reports from Arkansas, Louisiana, and Mississippi suggest that beetles are infesting active cavity trees at higher than expected rates (F. L. Oliveria, pers. commun.). Thus, there is a likelihood that the phenomenon we have observed is a south-wide problem in areas where Red-cockaded Woodpeckers use loblolly and shortleaf pines for cavity trees.

ACKNOWLEDGMENTS

We thank S. Best, D. Bieber, D. Carrie, R. Mize, and R. Sandal, for records from the Davy Crockett and Sam Houston National Forests and The I. D. Fairchild and W. Goodrich Jones State Forests, and V. Peacher, W. Nettleton, and F. Oliveria for assistance with SPBIS records for the Angelina National Forest. We thank R. F. Billings, J. L. Hayes, J. A. Jackson, F. C. James, and B. R. Parresol for constructive comments leading to the improvement of an early draft of the manuscript.

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Wilson Bull., 107(1), 1995, pp. 93–121

THE AVIAN CECUM: A REVIEW

Mary H. Clench and John R. Mathias[1]

Abstract.—The ceca, intestinal outpocketings of the gut, are described, classified by types, and their occurrence surveyed across the Order Aves. Correlation between cecal size and systematic position is weak except among closely related species. With many exceptions, herbivores and omnivores tend to have large ceca, insectivores and carnivores are variable, and piscivores and graminivores have small ceca. Although important progress has been made in recent years, especially through the use of wild birds under natural (or quasi-natural) conditions rather than studying domestic species in captivity, much remains to be learned about cecal functioning. Research on periodic changes in galliform and anseriform cecal size in response to dietary alterations is discussed. Studies demonstrating cellulose digestion and fermentation in ceca, and their utilization and absorption of water, nitrogenous compounds, and other nutrients are reviewed. We also note disease-causing organisms that may be found in ceca. The avian cecum is a multi-purpose organ, with the potential to act in many different ways—and depending on the species involved, its cecal morphology, and ecological conditions, cecal functioning can be efficient and vitally important to a bird's physiology, especially during periods of stress. *Received 14 Feb. 1994, accepted 2 June 1994.*

The digestive tract of most birds contains a pair of outpocketings that project from the proximal colon at its junction with the small intestine (Fig. 1). These ceca are usually fingerlike in shape, looking much like simple lateral extensions of the intestine, but some are complex in structure. Within the Class Aves, ceca range in size from very long to very short, or they may be entirely absent (Table 1). Unlike the case in almost all mammals, most avian ceca are paired and of approximately equal length, with separate lateral or ventrolateral openings into the colon (rectum). In some species the openings are dorsal or ventral, and a few paired ceca share a common orifice, but the great majority open into the lateral colon opposite one another (McLelland 1989). There has been confusion over how the passage of material through cecal openings is controlled, but it is now believed that the interdigitating meshwork of villi at the cecal entrance act as a filter, excluding large particles and allowing only fluid and fine particles to be separated and pushed from the colonic contents into the ceca by colonic antiperistalsis (Duke 1986a). This villous meshwork exists even in species, such as the House Sparrow (*Passer domesticus*), with very small, possibly nonfunctional, ceca (Klem et al. 1983). In the few species with larger ceca that have been studied histologically in detail (domestic chickens, *Gallus,* other galliforms, and ducks, *Anas*; Calhoun 1954, Clarke 1978, Fenna and Boag 1974b, Mahdi and

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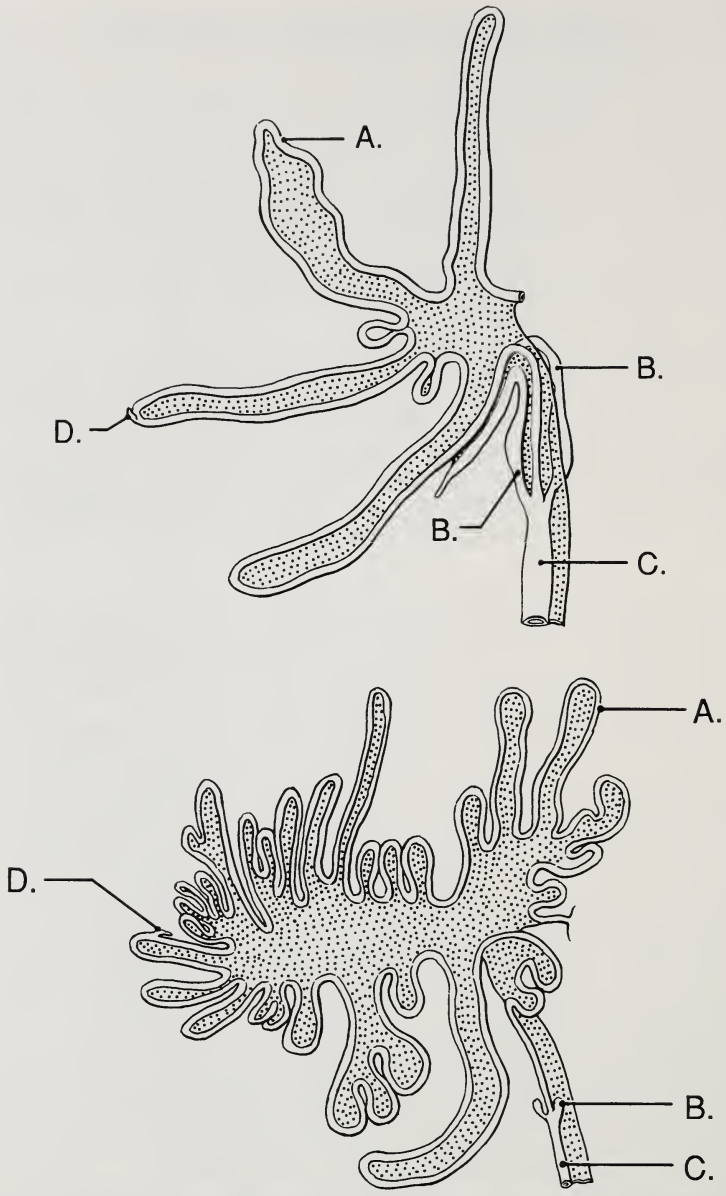

FIG. 1. Diagrammatic representation of avian digestive tracts distal to the stomach. (Top) Little Grebe (*Tachybaptus ruficollis*) and (Bottom) Jackass Penguin (*Spheniscus demersus*). (A) small intestine; (B) ceca; (C) colon; (D) Meckel's (vitelline) diverticulum. Redrawn from Mitchell (1901).

TABLE 1
CECAL CHARACTERISTICS BY ORDINAL GROUPS

	Size (paired)				
	Large	Moderate	Small/ vestigial	Absent	Remarks
Struthioniformes	X				
Rheiformes	X				
Casuariiformes		X			
Apterygiformes	X				
Tinamiformes	X				
Sphenisciformes			X		
Gaviiformes		X			
Podicipediformes		X	X		
Procellariiformes			X		Single in some spp.
					Variable, see text
Pelecaniformes			X		Single in some spp.
Ciconiiformes			X		Single in some spp.
		X			Phoenicopteridae
Anseriformes	X	X			*Mergus*: reduced
	X				*Chauna, Anhima*
Falconiformes			X		Some *Falco*: single
Galliformes	X				
Gruiformes	X				*Eurypyga*: small
Charadriiformes	X	X	X		Variable, see text
Columbiformes			X	X	Pteroclididae: large
Psittaciformes				X	
Cuculiformes	X	X		X	Variable, see text
	X				*Opisthocomus*
Strigiformes	X				
Caprimulgiformes	X				*Aegotheles*: absent
Apodiformes				X	
Coliiformes				X	
Trogoniformes		X			
Coraciiformes		X	X	X	Variable, see text
Piciformes				X	Galbulidae: small
Passeriformes			X		

McLelland 1988), the ceca have been found to have a well-developed basal ring of circular muscle forming a sphincter (not a flap valve, as some of the early literature suggested). The terminal ileum protrudes slightly into the proximal colon as an ileal papilla and also has a sphincter. From their bases, ceca usually extend orad on either side of the ileum and are loosely attached to it by mesentery and the ileocecal ligament. Certain birds, notably herons, have a single cecum. The Secretary-bird (*Sagittarius serpentarius*) has been reported, probably erroneously, to

have two pairs (Maumus 1902). Although the gross structure of most ceca is that of a simple blind-ended tube, others are morphologically complex; a few have internal folds or spirals, and in at least one species (Elegant Crested Tinamou, [*Eudromia elegans*]), the ceca contain multiple sacculations, resulting in structures that look much like two bunches of fused grapes.

As with many aspects of avian morphology, most ceca were described in the late 19th and early 20th centuries, the descriptions often being incidental to other studies. Of particular importance are the works by Beddard (1898), Mitchell (1901), and Maumus (1902). A later contribution to the field was made by Naik (1962), but only abstracts from that work (a thesis for an M.Sc. degree, Banaras Hindu Univ.) have been available in the published literature. Fortunately, a carbon copy of the thesis was sent to John McLelland who wrote a review of cecal gross anatomy (1989) and who has generously lent the thesis to us. Photocopies of Naik's important study of Indian birds, including histological descriptions and figures of the gross morphology of 80 species (33 families in 15 orders), have now been deposited in the Division of Birds Library, The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, and the Wilson Ornithological Society's Van Tyne Memorial Library at the Univ. of Michigan, Ann Arbor. Some of Naik's figures are included here (Fig. 2).

CECAL TYPES AND OCCURRENCE

Naik (1962) classified avian ceca into five histological types: (1) Intestinal—long ceca that are histologically similar to the small intestine, (2) Glandular—long and well-developed ceca with an abundance of glandular (especially goblet) cells and capable of profuse secretory activity, (3) Lymphoid—small ceca with many lymphocytes, (4) Vestigial—very small ceca, often embedded in the intestinal wall, with little or no lumen, and (5) Absent.

The following survey of the occurrence of cecal types by avian orders has been compiled from the relatively sparse available records. Unless otherwise noted, the information has been abstracted from Mitchell (1896a, 1901), Beddard (1898, 1911), Maumus (1902), Naik (1962), and McLelland (1989). We have also examined a few genera in alcohol-preserved specimens in the collections of The Carnegie Museum of Natural History (CM) and the National Museum of Natural History, Smithsonian Institution (USNM). Although we have not listed all the species for which ceca have been described, the genera whose ceca have been figured are specified at the end of each ordinal account. Cecal types are as given by Naik (1962); those he did not examine are noted with a (?). Cecal sizes

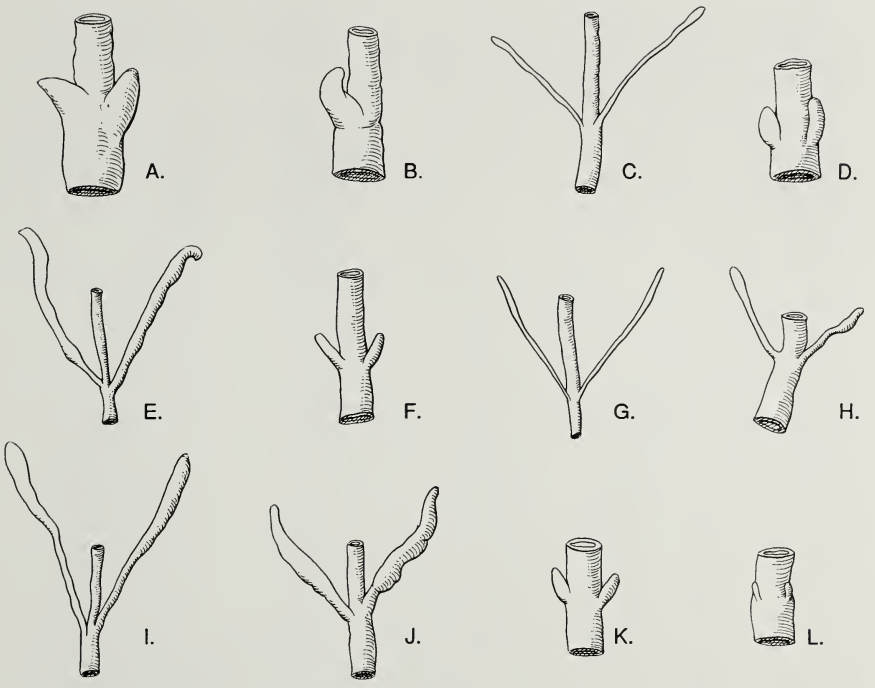

FIG. 2. Avian ceca: (A) Little Cormorant (*Phalacrocorax niger*), (Pelecaniformes) ×2.4; (B) Cattle Egret (*Bubulcus ibis*), (Ciconiiformes) ×2.4; (C) Cotton Teal (*Nettapus coromandelianus*), (Anseriformes) ×1.2; (D) Crested Serpent Eagle (*Spilornis cheela*), (Falconiformes) ×2.4; (E) Common Quail (*Coturnix coturnix*), (Galliformes) ×1.2; (F) Collared Dove (*Streptopelia decaocto*), (Columbiformes) ×3.2; (G) Redwattled Lapwing (*Vanellus indicus*), (Charadriiformes) ×0.8; (H) Common Koel (*Eudynamys scolopacea*), (Cuculiformes) ×2.0; (I) Spotted Owlet (*Athene brama*), (Strigiformes) ×1.2; (J) Indian Roller (*Coracias benghalensis*), (Coraciiformes) ×1.6; (K) Oriental Skylark (*Alauda gulgula*), (Passeriformes) ×4.0; (L) Gray Wagtail (*Motacilla cinerea*), (Passeriformes) ×3.2. Redrawn from Naik (1962), relative sizes indicated.

("large," "small") are relative to body sizes. With a few exceptions (e.g., *Opisthocomus*), the taxonomy followed is that of Morony et al. (1975).

Struthioniformes.—Intestinal type (?) Large and very long ceca (56–95 cm), externally fingerlike with a tapering tip and a well-developed internal valve-like helical fold that is reflected in the spiral shaping of the organ's exterior. The cecal wall is thin at the base, but thickens toward the apex. Although ostrich ceca are paired, they have a common orifice into the dorsal colon. This single cecal opening is present in all ratites. The ostrich colon is also very long (1640 cm), partly sacculated, and looped, unlike that of almost all other birds. Mitchell 1896a, Maumus 1902, Bezuidenhout 1986, *Struthio.*

Rheiformes.—Intestinal type (?) Even longer (42–142 cm), the ceca of rheas have less internal spiral folding than in ostriches; the colon is also long. Mitchell 1901, Maumus 1902, *Rhea.*

Casuariiformes.—Intestinal type (?) For large-bodied ratites, cassowaries have ceca that are relatively short (8–18 cm), but with sacculations; the colon is also short (29 cm; Herd and Dawson 1984, Herd 1985). Mitchell 1896a, *Casuarius.*

Apterygiformes.—Intestinal type (?) The ceca of kiwis are comparatively large (18 cm) and relatively wide, with less sacculation than in ostriches or rheas. Mitchell 1901, Maumus 1902, *Apteryx.*

Tinamiformes.—Intestinal type (?) Tinamou ceca are long (6–24 cm) and externally simple and fingerlike in *Tinamus, Crypturellus* (Fig. 3), and *Nothura.* We have externally examined, but not dissected, Brushland Tinamou (*Nothoprocta cinerascens*) (CM A-2369) and Small-billed Tinamou (*Crypturellus parvirostris*) (CM A-5330) and also found them simple. In contrast, the ceca of *Rhynchotus* are long, with an internal spiral structure; this is reflected in their external morphology.

The paired ceca of the Elegant Crested Tinamou are extraordinary and probably unique within Aves (Fig. 3): long and wide (12.5–13.0 × 2.2–2.5 cm; Wetmore 1926) and internally honeycombed by many small diverticula. These outpocketings gradually diminish in size and organization from the base to the tip of the organ, apically showing a more spiral form of internal ridges like ratite ceca. Externally, the basal diverticula protrude from the ceca as pointed lobes, gradually becoming flatter but still clearly apparent toward the organ's tip. Beddard 1890a, *Eudromia*; Beddard 1898, *Nothura*; Mitchell 1901, Maumus 1902, *Rhynchotus.*

Sphenisciformes.—Vestigial type (?) Penguin ceca are very small to vestigial (2–4 cm), whereas the small intestine is very long (178 ± 16 cm in chicks of the Gentoo Penguin, *Pygoscelis papua*; Roby et al, 1989). Mitchell 1896a, *Eudyptes*; Mitchell 1901, *Spheniscus* (Fig. 1), *Aptenodytes.*

Gaviiformes.—Intestinal type (?) Loons have moderately short (4–5 cm) and slender ceca with irregular internal sacculations. Mitchell 1896a, 1901, *Gavia.*

Podicipediformes.—Intestinal type (?) Grebe ceca are small (3–4 cm in *Podiceps,* but longer in *Tachybaptus*) and structurally apparently like those of loons. Mitchell 1901, *Podiceps*; Mitchell 1901, Beddard 1911, *Tachybaptus* (Fig. 1).

Procellariiformes.—Vestigial type (?) Ceca are generally small, nipplelike, or lacking (0–1 cm) in the tubenoses. Some species may have only one cecum, but in such cases one or both could have been overlooked, being obscured by fat or mesentaries or embedded in the intestinal

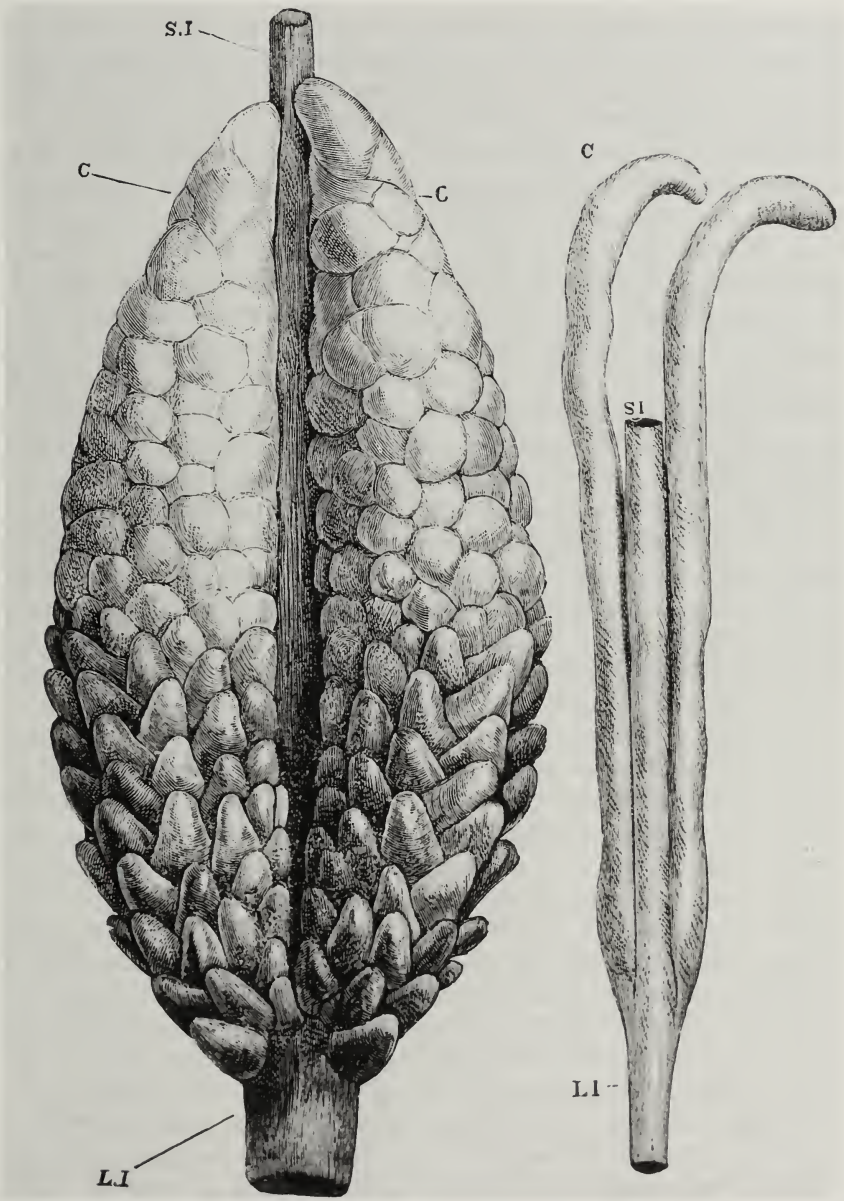

FIG. 3. Ceca of Elegant Crested Tinamou (*Eudromia elegans*) (left) and Spotted Tinamou (*Nothura maculosa*) (right). From Beddard (1898).

wall. However, G. Duke (pers. comm.) reports that Leach's Storm-petrel (*Oceanodroma leucorhoa*) has a single, relatively large cecum that is nearly as long as its colon. Mitchell 1896a, *Fulmarus*; Mitchell 1901, *Diomedea*; Kuroda 1986, *Pterodroma, Puffinus.*

Pelecaniformes.—Lymphoid type. The ceca of totipalmate swimmers are small (0.5–5 cm) in Pelecanidae and Phalacrocoracidae, and vestigial (<0.5 cm) in Phaethontidae, Sulidae, and Fregatidae. Only one cecum is visible in some specimens, although a second may be present. Mitchell 1901, *Phaethon, Sula, Phalacrocorax, Anhinga* (single cerum), *Fregata, Pelecanus*; Maumus 1902, *Pelecanus*; Naik 1962, *Phalacrocorax* (Fig. 2).

Ciconiiformes.—Lymphoid type. The ceca of herons and their allies are variable: reduced, small, or rudimentary in all but flamingos. Species with paired ceca often have one smaller than the other. Ciconiidae have two small ceca (0.3–1.5 cm); Scopidae also have two, as do Threskiornithidae (0.3–1.0 cm). Ardeidae usually have a single small cecum (0.4–1.0 cm), although careful examination may reveal a second rudimentary one in the wall of the intestine. Balaenicipitidae also have a single cecum. Phoenicopteridae, in contrast, have a relatively well-developed (8 cm) fingerlike pair, probably of the intestinal type. Mitchell 1896a, *Ciconia, Platalea*; Mitchell 1901, *Ardea, Nycticorax, Phoenicopterus, Mycteria, Scopus*; Maumus 1902, *Leptoptilos, Cochlearius, Mycteria, Ardea*; Naik 1962, *Anastomus, Bubulcus* (Fig. 2), *Nycticorax, Egretta, Ardeola.*

Anseriformes.—Intestinal type. The ceca of ducks and geese are generally moderate to long (4–38 cm), with exceptions such as reduced paired (0–5 cm), single, or absent ceca in *Mergus* and *Melanitta* (Goudie and Ryan 1991). Barnes and Thomas (1987) found a correlation between anatid cecal size (mass) and diet: herbivores have larger ceca than carnivores, and omnivores are intermediate. The screamers (*Chauna,* Anhimidae) are a major exception in that the ceca are large (8 cm), almost bulbous in appearance, sacculated internally, and followed by a large looped colon. *Anhima* has similar, but smaller, ceca. Mitchell 1896a, *Cygnus, Chauna*; Beddard 1898, *Chauna*; Mitchell 1901, *Mergus, Anseranas, Anas, Nettapus, Anhima*; Maumus 1902, *Mergus, Anas, Chauna*; Naik 1962, *Anas, Nettapus* (Fig. 2); Mattocks 1971, *Anser*; McLelland 1991, *Anas.*

Falconiformes.—Lymphoid type. The ceca of eagles, hawks, vultures, and other birds of prey are very small, vestigial, or absent (0–2 cm). Mitchell 1896a, *Haliaeetus*; Mitchell 1901, *Cathartes* (ceca absent), *Neophron, Gypohierax, Polyborus, Circus, Falco, Pandion*; Maumus 1902, *Accipiter*; Beddard 1911, *Polemaetus, Cathartes*; Naik 1962, *Milvus, Neophron, Gyps, Spilornis* (Fig. 2).

Mitchell's figure (1901) of the Secretary-bird, does not include the lower colon where Maumus (1902) recorded finding a second pair of ceca.

Beddard (1898) examined four specimens of *Sagittarius* and noted nothing unusual about their ceca (0.4–0.6 cm long), nor did he mention a second, distal pair. Maloiy et al. (1987) reported that two specimens they examined had a single pair of very small "cecal buds;" one specimen is figured. In light of these studies, the otherwise unremarkable intestinal tract of the Secretary-bird as discussed in detail by Mitchell (1901), and the generally poor cecal development of the Falconiformes, we are inclined to believe that Maumus mistook an anomaly or perhaps a pathological condition for a (figured) budlike "second pair" of ceca 9 cm from the cloaca; a "normal" pair, figured as having a long thin stalk with a greatly expanded tip, was 125 cm proximal to the cloaca and in the usual location for ceca.

Galliformes.—Intestinal type. The best developed of the intestinal type, gallinaceous ceca range from long to very long (6–34 cm), with extreme lengths of 35–92 cm in certain grouse in winter (Moss 1983). The ceca usually widen apically or end in a bluntly rounded tip rather than tapering at the apex and may contain internal submucosal folds. The Satyr Tragopan (*Tragopan satyra*) is the only galliform known to have sacculated ceca (McLelland 1989). Beddard (1911) described the Crested Bobwhite (*Colinus cristatus*) ("*Eupsychortyx sonnini*") as having ceca that were spirally coiled and covered by a loosely meshed network of bands containing a great deal of fat. We suspect this quail had seasonally enlarged ceca, as is now known to occur in many other galliforms. Mitchell 1896a, *Argusianus*; Mitchell 1901, *Alectura, Crax, Pavo*; Maumus 1902, *Numida*; Beddard 1911, *Alectura*; Leopold 1953, *Callipepla*; Naik 1962, *Coturnix* (Fig. 2), *Gallus.* Peckham (1965) reported a cecal anomaly in *Gallus*: a chicken with a single cecum that was bifurcated at the tip.

Gruiformes.—Intestinal type. The diverse order of cranes, rails, and allies has generally large ceca (2.5–37.0 cm), with the exception of the Sunbittern, *Eurypyga helias* (0.6 cm). In the Otidae (*Otis* [27 cm], *Coriotis* [24 cm], and *Eupodotis*), the long cecum is unusual: the basal third has internal villi; the middle third is dilated, lined with a smooth mucous membrane, slightly partitioned by longitudinal folds (but no sacculations) and scattered with many glands; and the apical third has a netlike mucous membrane. Most of the gruiform families have been described. Mitchell 1896a, *Crex, Cariama*; Mitchell 1901, *Turnix, Tricholimnas, Grus, Aramus* (only 5–8 cm long, but wide), *Psophia, Otis, Rhynochetos, Heliornis*; Maumus 1902, *Otis, Porphyrio, Aramides*; Beddard 1911, *Eupodotis*; Naik 1962, *Amaurornis, Turnix*; Sitna 1965, *Fulica*; Maloiy et al. 1987, *Choriotis.*

Charadriiformes.—Intestinal type. Shorebird ceca are variable: rudimentary in Jacanidae, some Scolopacidae (*Scolopax, Eurynorhynchus*),

Laridae (short in *Anous* but long in *Gygis*), Rhynchopidae, and Alcidae (but 3 cm in *Alca*); moderately large (2–9 cm) in Hematopodidae, Recurvirostridae, Burhinidae, Glareolidae, Charadriidae, most Scolopacidae, Thinocoridae, and Stercorariidae; and very large (21–23 cm) in sheathbills, Chionidae. The long ceca are fingerlike in shape and frequently tapered at the tip. Mitchell 1896a, *Numenius, Scolopax, Larus*; Mitchell 1901, *Calidris, Chionis, Glareola, Thinocorus, Jacana, Pagophila, Stercorarius, Sterna, Fratercula, Uria*; Maumus 1902, *Alca, Numenius*; Beddard 1911, *Pluvianus, Fratercula*; Naik 1962, *Vanellus* (Fig. 2).

Columbiformes.—Lymphoid or vestigial types. Ceca are very small or (mostly) entirely absent in pigeons (Columbidae) but large (intestinal type?) with internal folds and a common orifice into the colon in sandgrouse (Pteroclididae; 12 cm in *Syrrhaptes*). Mitchell 1896a, *Pterocles, Columba*; Maumus 1902, *Pterocles*; Naik 1962, *Columba, Streptopelia* (Fig. 2); McLelland 1991, *Columba.*

Psittaciformes.—Ceca are entirely absent in parrots, without a trace in embryos or adults. Mitchell 1896a, *Ara*; Mitchell 1901, *Strigops*; Beddard 1911, *Nestor.*

Cuculiformes.—Intestinal type. The ceca of cuckoos (Cuculidae) are moderate to long (2–6 cm in most, 17 cm in *Scythrops*) but absent in touracos (Musophagidae). The tip is expanded in roadrunners, *Geococcyx.*

The large ceca of *Opisthocomus* are like those of gallinaceous birds but also like those of cuckoos. Other parts of the Hoatzin's digestive tract show extreme specializations—a large crop that has been demonstrated to digest vegetation (Grajal et al. 1989) and a long colon with convolutions (of unknown function) similar to those of ratites and *Chauna.* Mitchell 1896a, *Tauraco*; Mitchell 1896b, *Opisthocomus*; Mitchell 1901, *Carpococcyx*; Maumus 1902, *Opisthocomus*; Marshall 1906, *Geococcyx*; Naik 1962, *Eudynamys* (Fig. 2), *Clamator, Centropus*; Grajal et al. 1989, *Opisthocomus.*

Strigiformes.—Glandular type. The ceca of most owls are generally large (4–11 cm) and distinctively shaped: the apical half is expanded to a greater or lesser degree. An extreme example of this differentiation is found in *Phodilus* (Beddard 1890b), where each cecum is a bulbous organ at the end of a thin, stalk-like tube that connects it to the colon. We have briefly examined a preserved *Tyto alba* (CM A-24479): each cecum looks like a swollen leaf with a narrow stalk-like base and a greatly expanded, clearly glandular apex that has the superficial appearance of bleached liver. Judging from the conflicting descriptions of owl ceca in the literature, the degree of apical dilation may be individually variable, with some specimens showing little or no expansion. The recorded variation in owls may be seasonal (like expanded grouse ceca in winter) or it may be a

response to other dietary or environmental changes. Mitchell 1896a, Marshall 1906, *Bubo*; Mitchell 1901, Maumus 1902, *Strix, Asio*; Beddard 1911, *Asio*; Naik 1962, *Tyto, Bubo, Athene* (Fig. 2), *Glaucidium.*

Caprimulgiformes.—Glandular type (?) Nightjars (Caprimulgidae) and frogmouths (Podargidae) have large (3–5 cm) ceca, the apical half dilated like those of some owls. Oilbirds (*Steatornis*) are also reported to have long paired ceca (Bosque and de Parra 1992). Owlet-frogmouths (Aegothelidae) lack ceca. Mitchell 1901, *Nyctidromus*; Marshall 1905, *Phalaenoptilus.*

Apodiformes.—Ceca are absent in both swifts and hummingbirds. Mitchell 1901, *Apus*; Marshall 1906, *Aeronautes.*

Coliiformes.—Colies also lack ceca. Mitchell 1896a, *Colius.*

Trogoniformes.—Intestinal type (?) Trogon ceca are moderate in length (3–5 cm). Mitchell 1901, *Trogon.*

Coraciiformes.—Intestinal, glandular (*Coracias*), or absent types. Most of the kingfishers and allies lack ceca: Alcedinidae, Momotidae, Upupidae, Phoeniculidae, and Bucerotidae. In the other families (so far as is known), the ceca are apically dilated like those of owls. They are short (1–3 cm) but wide in bee-eaters and todies (Meropidae and Todidae); in the Puerto Rican Tody (*Todus mexicanus*) (CM A-832) the ceca are 7 mm long and about 1 mm wide, slightly broader at the apex. Rollers and cuckoo-rollers (Coraciidae and Leptosomatidae) have long ceca (4–7 cm). Mitchell 1896a, *Aceros*; Mitchell 1901, *Coracias, Dacelo, Merops, Upupa*; Naik 1962, *Merops, Coracias* (Fig. 2).

Piciformes.—With the exception of jacamars (Galbulidae), which have short (2 cm) ceca, the organ is absent in all families of woodpeckers and allies, including honeyguides and puffbirds (Indicatoridae and Bucconidae: Lesser Honeyguide [*Indicator minor*], USNM 290581; Spotted Puffbird [*Bucco tamiata*], CM A-1308). Beddard (1898:186) noted that ceca are "exceptionally present" in the Eurasian Green Woodpecker (*Picus viridis*) and he later (1911) figured a specimen lacking ceca, but it is generally true that in species that normally lack ceca, individuals are occasionally found with vestigial organs. Mitchell 1901, *Megalaima*; Beddard 1911, *Melanerpes.*

Passeriformes.—Lymphoid or vestigial types. Passerine ceca are small or rudimentary and nipple-like (<0.1–1.5 cm) but apparently never completely absent. The ceca have thick walls and a very small lumen. In the largest passerine, the Superb Lyrebird (*Menura novaehollandiae*) (CM A-1834), the ceca are 1.2 cm long and 0.3 cm wide. Mitchell 1896a, *Parus*; Mitchell 1901, *Corvus*; Maumus 1902, *Poephila*; Beddard 1911, *Gymnorhina*; Klem et al. 1983, *Passer*; Klem et al. 1984, *Turdus*; McLelland 1991, *Serinus.* Naik (1962) figured 35 species (26 genera) in 14 passerine

families (taxonomy as used by Naik): Alaudidae (1; *Alauda,* Fig. 2), Laniidae (1), Oriolidae (1), Dicruridae (1), Sturnidae (6), Corvidae (3), Campephagidae (2), Pycnonotidae (2), Muscicapidae (5), Motacillidae (4; *Motacilla,* Fig. 2), Nectariniidae (2), Ploceidae (5), Fringillidae (1), and Emberizidae (1); all specimens had small paired ceca, ranging from 0.05 to 1.15 cm in length.

This ordinal summary demonstrates that correlation between cecal size and systematic position is weak except among closely related species. However, since the early studies (e.g., Mitchell 1901), workers have noted a general relationship between cecal development and diet. In broad terms, herbivores have larger ceca and carnivores have smaller ones. Naik (1962) observed that ceca tend to be well-developed in Indian herbivores, omnivores, and birds that feed on molluscs (but see Goudie and Ryan 1991); they are variable in insectivores and carnivores and small in piscivores and graminivores (McLelland 1989). However, on a world-wide basis, the exceptions are many. For instance, hawks and owls with basically similar carnivorous diets have ceca of very different sizes and histologies. Fish-eating species fall into several different cecal size categories: loons and grebes have relatively well-developed ceca, penguins have small-to-vestigial ones, and kingfishers have none at all. Insectivores range from large-to-moderate ceca in nightjars, trogons, and bee-eaters, through small-to-vestigial in insectivorous passerines, and are absent in swifts and hummingbirds. It is probable that dietary changes resulting from such variables as seasonal availability of food types, individual preferences, and age effects strongly modify genetic influences on cecal structure. Non-dietary factors also may be more important than food in some species.

CECAL FUNCTIONS

Cecal functioning is still only partly understood (McNab 1973, Braun and Duke 1989). Although early investigations searched for a single function of the organ, it is now clear that the cecum has the potential to act in many different ways. And depending on the species involved, the cecal morphology, and the ecological conditions under which a bird lives, those functions can be vitally important to its physiology—perhaps especially so during periods of stress. It is also apparent that the avian cecum *can* function in a highly efficient manner, even more efficiently than the cecum of most mammalian herbivores in terms of size and fermentation rates (Gasaway 1976b).

The intestinal type of cecum in birds is a blind-ended sac with a meshwork of long interdigitating villi at its entrance. The majority of cecal villi apparently act as a sieve, allowing fluid and fine particles to enter

the cecal lumen as colonic contents are pushed against and selectively past the cecal sphincter by retrograde waves of colonic muscle contraction (Fenna and Boag 1974a). At the same time, this material is prevented from moving up into the ileum by the contracted ileal sphincter. The colonic motility probably also rinses water-soluble substances and fine particles from the colonic contents and pushes them into the ceca (Björnhag 1989). Because a cecum is blind-ended, its contents can be retained for longer periods than would be possible in the main (small or large) intestine through which digesta move relatively rapidly (e.g., Shibata and Sogou 1982, Clench and Mathias 1992). Held in the ceca, fluid has time to be absorbed and molecules in solution as well as solid particles can be acted on by bacteria, fungi, and other micro-organisms (Duke 1986b). It is also now appreciated that the mixing action produced by cecal wall contractions keeps the contents in general motion; cecal motility also contributes to filling and evacuating the organ (Duke 1986a, Clench and Mathias, unpubl. data). Thus, at different times and under different conditions, the cecum has been found to be a site for fermentation and further digestion of food (especially for breakdown of cellulose), for utilization and absorption of water and nitrogenous components, for microbial action of both beneficial and disease-causing organisms, and as a site for production of immunoglobulins and antibodies.

Study subjects.—Much of what is known about cecal physiology is based on studies of gallinaceous birds and waterfowl: the intestinal type of cecum. These birds (and their ceca) are large enough to study easily. Domestic and semidomestic species (chickens, quail, pheasants; domestic ducks and geese) also are readily available, they are behaviorally more amenable to manipulation, and their economic importance leads to research funding. Unfortunately, however, most domestic birds (notably chickens) have proved to be exceptionally poor models for the study of cecal function. This is probably because, through the genetic changes resulting from domestication, and the almost universal use of commercial, nutritionally complete, poultry feed (even "enhanced" with antibiotics), the average chicken cecum has lost much or all of its natural microflora and -fauna and its potential physiological capabilities (Thomas 1987). A chicken fed on whole natural grains that require more "digestion" produces results more like those from wild birds (unpubl. data). A cecectomized chicken seldom differs significantly from the intact bird in growth or other physiologic indicators (Thornburn and Willcox, 1965). Consequently, older literature abounds with contradictory and confusing reports based on studies of domestic fowl (McNab 1973). A clearer picture of natural cecal function is only now beginning to emerge.

Because some popular game species—grouse, ptarmigan, and allies

(Tetraoninae)—undergo spectacular annual cecal changes, the study of their digestive system is both economically important and theoretically interesting. However, domesticated individuals of wild species, or even birds recently captured from the wild, may produce data that are significantly different from data obtained from the natural condition. For example, Moss (1972) used Red Grouse (*Lagopus lagopus scoticus*) to show the striking effects of captivity on cecal length. The mean cecal (combined) length from 29 wild males was 144 cm, whereas measurements from birds raised from eggs taken from natural nests were significantly shorter. Cecal lengths continued to decrease each generation the grouse were away from the wild, and ceca were 54% shorter than those of wild birds by the fourth year, when the experiment ended. Many other studies (e.g., Moss and Parkinson 1972; Moss 1974, 1977; Hanssen 1979a) have also demonstrated major differences in gut length and digestive capability in the ceca of wild vs captive galliforms.

Ceca in captives and domestic birds usually have a poorer microfauna and -flora than those of wild individuals. Hanssen (1979a, b) showed that cecal microanatomy and -biology of wild vs captive Willow Grouse (*L. l. lagopus*) were very different. Additionally, unless ceca are allowed sufficient time to adjust to changes in diet or other variables being studied, results may not be physiologically accurate. Subjects are often allowed only a few days to a week to adapt to a new diet (e.g., Inman 1973), when it may take considerably longer than that—4 to 12 weeks—for acclimatization (Savory and Gentle 1976, Moss 1977, Kenward and Sibly 1978, Duke et al. 1984, Moss 1989, Redig 1989). The common use of domestic birds with a limited cecal microbiota has also seriously handicapped attempts to apply principles obtained from those studies to cecal functioning in wild species. Moss (1989:61) suggested that galliform digestion may function in two modes: "1) a low-fiber mode, in which bulk does not limit intake and fiber digestion is unimportant, and 2) a high-fiber mode, in which bulk limits intake and fiber digestion may well be important." He also noted (loc. cit.) that "most studies on avian digestion have been of captive galliforms, most of which probably function in low-fiber mode all the time. Wild galliforms seem to function in high-fiber mode for much of the time. . . ." The low-fiber mode includes shorter, unmodified ceca that are probably unnecessary for digestion of artificial diets. However, Moss also showed that certain intestinal tract data from captives fell onto the same regression lines as those from free-living wild birds, indicating that some information could be usefully extrapolated from one to the other.

Diet and changes in cecal length.—Considerable research, particularly with anseriform and galliform species, has been conducted on how diet

affects cecal size. Captives have often been used to demonstrate different dietary effects on cecal length and mass (e.g., Mallards [*Anas platyrhynchos*]; Miller 1975, Kehoe et al. 1988). Wild birds have also been used in the same sorts of studies. For example, Sitna (1965) compared small samples of captive vs wild Eurasian Coots (*Fulica atra*). Her birds were kept for >16 months on diets of plants, starch, or fish, and all had shorter ceca (15.6 to 18.8 cm) than those of coots collected from the wild (24.2 cm).

Particular attention has been paid to the increase in grouse cecal lengths and masses in winter, when the birds are feeding on a poorer, more fibrous diet. Although cecal lengths and masses do not measure the same thing, they do indicate a general size increase. It is unknown, for instance, whether heavier ceca result from muscle hypertrophy or cell proliferation (of any type), or if cecal lengthening is produced by cell proliferation or is a simple distention of an elastic organ in response to more bulk in the lumen.

Mortensen et al. (1985) showed that in Norwegian Rock Ptarmigan (*Lagopus mutus*) ceca more than doubled in mass, from 22 g in September to a peak of 48 g in March. Thomas (1984) found that in Willow Ptarmigan (*L. lagopus*) in Ontario, winter cecal masses of males were 10.2 ± 3.0 g, but then decreased to 5.5 ± 0.6 g in spring; females were similar, going from 9.1 ± 1.9 g to 5.7 ± 0.6 g. The ceca also were much longer in winter, with a combined length of 119.4 ± 10.8 cm in males and 114.0 ± 7.6 cm in females. The same species in Finnish Lapland may have even longer winter ceca—140.0 ± 10.0 cm in males, 129.7 ± 7.2 cm in females (Pulliainen and Tunkkari 1983). Pulliainen (1976) also showed in a sample of 282 birds that *L. lagopus* in Lapland have winter ceca longer than the small intestine—124.5 ± 1.1 cm and 93.8 ± 0.6 cm, respectively. Even the ceca of California Quail (*Lophortyx californicus brunnescens*) living in a moderate climate, but where the winter diet is exclusively low-quality bulky greens, lengthen from 8 cm in summer to 12.5 cm in winter; the villi also increase in length at the same time (Lewin 1963). Pendergast and Boag (1973) showed that the ceca of wild male Alberta Spruce Grouse (*Canachites canadensis*) were also significantly longer and heavier ($P < 0.01$) in winter—410 mm in February vs 340 mm in April. However, captives from the same population that were maintained mostly on poultry feed did not have the same size or degree of seasonal change—270 mm vs 170 mm, winter vs summer. Moss (1989) has shown that cecal lengthening in response to an increase in dietary fiber is not linear; significant lengthening occurs only after a critical percentage of fiber in the diet has been reached.

In wild North American Anatidae, Barnes and Thomas (1987) found

that a guild of six carnivorous duck species had significantly smaller ceca ($P < 0.0001$) than three omnivorous species with intermediate-sized organs that, in turn, differed significantly ($P < 0.0001$) from nine herbivores with large ceca. Gizzard and small-intestine masses reflected the same differences. Kehoe and Ankney (1985) reported that in five species of diving ducks (*Aythya*), cecal length was greatest in *A. americana,* intermediate in *A. affinis, A. collaris,* and *A. marila,* and least in *A. valisineria,* which directly correlated with the amount of fiber in their respective diets. Goudie and Ryan (1991) noted that Black Scoters (*Melanitta nigra*), feeding almost exclusively on mussels (*Mytilus edulis*), had very short ceca (ca 2 cm) compared with four other sea duck species with more diverse diets. Paulus (1982) reported that both sexes of Gadwalls (*Anas strepera*) had heavier ceca in January and February, when they were feeding on higher-fiber foods, than they had in November. Halse (1984, 1985) found seasonal changes in Egyptian Geese (*Alopochen aegyptiacus*) and Spur-winged Geese (*Plectropterus gambensis*): the ceca hypertrophied significantly ($P < 0.05$) during the wing molt when the birds were flightless and their main diet changed from corn to water plants. Drobney (1984) reported that cecal lengths of female Wood Ducks (*Aix sponsa*) increased between the fall courtship and egg-laying periods ($P < 0.001$), whereas those of males decreased during the same period ($P < 0.001$). In contrast, Ankney and Afton (1988) found no difference in prelaying vs laying-period cecal lengths and masses in male and female Northern Shovelers (*Anas clypeata*); they noted also that shovelers are relatively more carnivorous than other waterfowl. In all these studies of anseriforms, it was concluded that the gut changes resulted from a complex of factors, especially (but not always) an increase in dietary fiber and differences in quantity of food consumed.

Digestion and fermentation.—A convincing demonstration of cellulose digestion, fermentation, and absorption of nutrients from avian ceca has taken many years (McNab 1973). This delay may have resulted largely from the study of domestic fowl lacking dietary preconditioning and appropriate bacteria (Gasaway 1976b, Duke et al. 1984). The process of collecting and culturing anaerobic microorganisms, even from wild birds with abundant cecal faunas, is also difficult (McBee and West 1969, Jayne-Williams and Fuller 1971). Only by study of wild birds, especially grouse, have some of the basic questions on cecal digestion begun to be answered.

The first proof that cecal bacteria could decompose cellulose was reported from the Eurasian Capercaillie (*Tetrao urogallus*) and Willow Grouse (*L. lagopus*) by Suomalainen and Arhimo in 1945. Shortly thereafter, Leopold (1953) suggested a relationship between intestinal length

and diet: the ceca of grouse that fed on low-quality, high-fiber browse averaged 136% longer than those of seed-eating galliforms. At the time, Leopold apparently did not realize that galliform ceca can lengthen in winter. By the late 1960s, cellulose digestion and fermentation in wild birds had become an active field of study, but some investigations were still marred by insufficient preconditioning before birds were fed new diets.

One of the first studies to demonstrate effective cecal fermentation used Alaskan Willow Ptarmigan (*L. lagopus*) (McBee and West 1969). In winter, this species feeds almost entirely on willow (*Salix*) twig tips and buds. In processing the food, gizzard action grinds the buds but it strips and grinds only the bark and cambium layers from the twigs. After passing down the small intestine, almost all the relatively nutritious and finely ground bud-bark-cambium paste is diverted into the ceca; the well-cleaned but undigested woody cores are passed into the colon for evacuation. Measurable amounts of fermentation products—lactic, acetic, propionic, and butyric acids and ethanol—were found only in the ceca, which were also the only site for significant numbers of bacteria, an average of 1.4×10^{11}/g of cecal contents (wet weight). The bacteria were difficult to culture, but anaerobes appeared to dominate—38.8% gram-positive rods, 47.9% gram-negative spirals or rods, and 13.6% gram-positive and -negative cocci. The authors estimated that 6% to 30% of the basal energy requirement of Willow Grouse in winter was supplied by cecal fermentation.

The contribution of ceca to avian nutrition has continued to be studied not only in grouse but also in waterfowl and other groups: Mattocks 1971, Moss and Parkinson 1972, Inman 1973, Thompson and Boag 1975, Miller 1976, Gasaway 1976a–d, Moss and Hanssen 1980 (review), Moss 1983, Herd and Dawson 1984, Buchsbaum et al. 1986, Dawson et al. 1989. Details of these studies cannot be included here, but in general they have shown that in species with well-developed ceca, significant proportions of dietary cellulose are digested and absorbed. The variation in fiber digestibility depends mostly on how much of the fiber can be processed into fine particles that, with soluble components, enter the ceca. Once in the organ, virtually all the cecal fiber is digested (e.g., an average of 96.8% in Blue Grouse, *Dendragapus obscurus*; Remington 1989).

Although almost all birds that include fermentation in their digestive processes do so in the ceca, a few have been shown to ferment food in other parts of the gut. Emus (*Dromaius*) have relatively short ceca but can ferment significant amounts of plant fiber in the distal small intestine and, to a lesser extent, the colon (Herd and Dawson 1984, Herd 1985). The South American Hoatzin (*Opisthocomus hoazin*), a rare avian foli-

vore, is the only bird known to ferment in the foregut; it has a specialized crop and esophagus in which the leaves that it feeds on are ground up and retained for long periods of time (~2 days) while cell walls are digested. The Hoatzin also, however, employs its large ceca for additional microbial fermentation (Grajal et al. 1989). New Zealand's Kakapo, *Strigops habroptilus,* is another avian obligate folivore, and like the Hoatzin, it has a specialized foregut. But unlike the Hoatzin, the nocturnal parrot probably cannot digest cellulose, relying instead on the extraction of cell contents from large quantities of vegetation (Morton 1978). As with all parrots, the Kakapo lacks ceca. Birds that primarily feed on vegetation either employ cecal fermentation or their digestive systems simply strip the easily obtained nutrients from plant material and quickly discard the rest. The New Zealand Takahe (*Notornis mantelli*) lacks morphological gut specializations and processes astounding amounts of grass. Reid (1974) reported that an adult Takahe can daily void ~8 m of feces from a gut that is <1.5 m long! Carrying a heavy load of digesting plant material is a serious drawback for flight efficiency, so it is not surprising that probably <3% of bird species are regular herbivores, and those that depend on bulky food are mostly or entirely flightless (Dawson 1989). Hoatzins are very poor fliers (pers. obs., M.H.C.). When grouse have expanded ceca in winter they fly poorly and reluctantly, and Emus, Kakapos, and Takahes are entirely flightless.

Utilization and absorption of water and nitrogenous compounds.—As investigations into cecal contents have become more detailed, and especially as their chemical processes have been analyzed, more attention has been paid to cecal functions in relation to fluids (e.g., salt and water balance, urine breakdown). The level of knowledge has now progressed to the point that absorption of fluids rather than nutrition has been suggested as the primary function of ceca in some species.

A landmark paper by Browne (1922) showed that fluid moved from the cloaca through the colon and into the ceca. It is now known that normal antiperistaltic motility of the colon moves its luminal fluids, including urine from the cloaca, proximally toward, and usually into, the ceca (but not the small intestine). This colonic antiperistalsis has been shown in Emus, various herons, ducks, geese, hawks, galliforms, gulls, roadrunners, owls, and crows (*Corvus*) (Akester et al. 1967, Ohmart et al. 1970, Clemens et al. 1975, Duke et al. 1984, Björnhag 1989). Many other (unstudied) birds probably also have this capability, but not all, even desert-dwelling species, do: an Australian cockatoo, the Galah (*Eolophus roseicapillus*) which, like all parrots, lacks ceca (Skadhauge 1976); some desert galliforms (Thomas et al. 1984); and ostriches (Skadhauge et al. 1984).

How important ceca are in the water balance of birds has been studied and debated for decades. It is now clear that the importance can vary with the species being studied, its age *and sex,* the degree of cecal development, and environmental stresses. Early studies of cecectomized chicks suggested that removal of the organ had no influence on water balance. But a later study of eight-month-old roosters showed that when more than two thirds of the ceca were removed, the birds drank significantly more water ($P < 0.05$) and produced 30% more fecal material, leading Isshiki and Nakahiro (1975) to conclude that ceca were important in water absorption, even in this domesticated species. Thomas (1982) noted that in birds with large ceca, water absorption occurs in ceca > colon > coprodeum. In a wild Alaskan galliform, the Rock Ptarmigan (*Lagopus mutus*), Gasaway et al. (1976) found that ceca were the major site of water absorption in the hindgut: 86% of water passing into the ileocecalcolic region was diverted into the ceca where virtually all (96%) of it was absorbed; 88% of the remaining 14% in the colon was passed out in feces. Gasaway et al. (1976) also noted, however, that the work of others had showed cecal water absorption to be less important in other wild galliforms (*Phasianus, Alectoris, Colinus*). Hughes et al. (1991) reported that the effects of cecal ligation differed in adult male and female domestic ducks when challenged by increased saline intake, but not when acclimated to fresh water.

When Duke et al. (1981) removed the glandular ceca of Great Horned Owls (*Bubo virginianus*), the birds drank more water during days 8–15 postoperatively, but then apparently compensated in some way for the cecal loss and returned to the same water intake levels as sham-operated birds had. This rapid compensation for cecectomy has also been shown in other species, leading to the conclusion that ceca were not vital to water balance, at least in most birds (Chaplin 1989). But when Chaplin measured the turnover of tritiated water in Great Horned Owls under low and high temperature conditions before surgical removal of the ceca and then again after allowing six weeks for recovery, she found water turnover was much higher. Excretory water loss was greatly increased (2.1× at 15°C and 4.8× at 27°C), but it could be offset by increased intake of food (rats) under 15°C and food and water under 27°C. Without supplementary food and water, the cecectomized birds could not maintain their body mass, and at 27°C also became dehydrated. Thus Chaplin (1989) concluded that ceca are vital to the water balance of those species that have them.

Assaying the microbiota contained in the cecal lumen has been another approach to studying cecal function (Barnes 1972, 1979). Most cecal faunal studies have been conducted in domestic fowl, demonstrating the pres-

ence of an abundant population of anaerobic bacteria: $\sim 10^{11}$/g, wet mass, in chickens, but almost as many ($>10^{10}$/g) in other domestic and wild galliforms and ducks (Mead 1989). In chickens, the main bacterial types are anaerobes: gram-positive cocci (28%), gram-negative Bacteroidaceae (20%), gram-positive *Eubacterium* sp. (16%), gram-positive *Bifidobacterium* sp. (9%), budding cocci (6%), *Gemmiger formicilis* (5%), *Clostridium* sp. (5%) and miscellaneous (11%) (Barnes 1972, 1979). Oxygen-tolerant bacteria, yeasts, molds, and protozoa are found in much lower numbers, but it is not surprising that cecal faunas differ from species to species and show a succession of species as the host ages (Mead 1989). Most cecal anaerobes ($\sim 10^{9}$/g in both domestic and wild birds) can degrade uric acid to volatile fatty acids and ammonia (Mead 1989).

It is well known that avian urine contains uric acid, but contrary to earlier assumptions, it is now known that little of this uric acid has a crystalline structure. Instead, it is in a supersaturated colloidal suspension with Na^+ and K^+ and matrix molecules, forming small (0.5–13 μm) spheres that pass easily through the renal duct system (Braun and Campbell 1989). After reaching the cloaca and refluxing into the lower bowel, these spheres are commonly found in the colonic fecal material, but they are rare in the cecal lumen as a result of their rapid degradation by cecal microbiota (Mortensen and Tindall 1981a, Braun and Campbell 1989). Anaerobic decomposition of uric acid has been reported to yield ammonia, acetate, CO_2, glycine, formate, propionate, complex molecules such as proteins and vitamins, and possibly alcohols; the volatile fatty acids produced are used in or absorbed by the ceca and provide an important energy source (Barnes and Impey 1974, Braun and Campbell 1989). Some of the ammonia released by breakdown of uric acid, urea, and amino acids from both dietary and urinary nitrogenous compounds is used in the production of glutamine and probably other amino acids (Mortensen and Tindall 1981b, Karasawa 1989, Mortensen 1984).

The chemical processes that occur in avian ceca, especially nitrogen cycling and nutrient transport, are still under active investigation. For many years, it was generally held that regardless of what was produced microbially in the cecum, transport across the cecal wall was too poor for the organ to be functionally important. Recent studies (e.g., Moretó and Planas 1989, Obst and Diamond 1989, Thomas and Skadhauge 1989) have shown this to be untrue. For example, using new techniques to measure the nutrient transport capabilities of a wide variety of domestic and wild species—chickens, Rock Doves (*Columba livia*), Canada Geese (*Branta canadensis*), Sage Grouse (*Centrocercus urophasianus*), and Red-necked Phalaropes (*Phalaropus lobatus*)—Obst and Diamond (1989) found cecal transport to exist in all five and to be well developed in most.

Transport varied by cecal region and approached or exceeded intestinal levels in the grouse and phalaropes. Ceca accounted for different amounts of the entire gut's integrated transport capacity: between 0.1% in Rock Doves (with vestigial ceca) and 49% in Sage Grouse (with the largest ceca that occur in tetraonids). Therefore, it is now clear that ceca can contribute in an important way to the nitrogen economy of galliforms and other birds with large functional organs, especially under poor nutritional conditions and other environmental stresses (Dawson and Herd 1983, Björnhag 1989, Braun and Duke 1989, Chaplin 1989).

Disease-causing organisms.—Because they are essentially bags of anaerobic bacteria, protozoa, fungi, and other micro- and macro-organisms, having a relatively constant pH of 6.0–6.5 (Hill 1971), ceca contain both beneficial and disease-causing forms; surprisingly few have been shown to be pathogenic. In addition, there is good evidence that the log-phase growth and subsequent invasion of bacteria such as *Salmonella typhimurium* may be prevented by anaerobes in the ceca (Barnes 1977).

Probably the most notable and pathogenic cecal micro-organism is *Eimeria tenella,* which causes severe bloody coccidiosis in birds, especially domestic fowl. As with many gastrointestinal pathogens, this one can alter cecal motility so that for about two days after infection, the host defecates few of the protozoans and their numbers proliferate. *E. tenella* causes extensive physical damage to cecal tissue (Clarke 1979).

Nematodes (roundworms, pinworms) are the most common macroscopic invaders, moving as swallowed larvae from the upper gut to the colon and into the ceca. Several different species are known to occur in galliforms and anseriforms (Wehr 1965, Watson et al. 1988), with young birds being especially susceptible to heavy nematode infections. The most serious parasitic species in wild birds appears to be *Trichostrongylus tenuis,* which can complete its life cycle without an intermediate host. *T. tenuis* attacks the cecal mucosa, causing anemia, low blood protein levels, increased anorexia, delayed and reduced egg production, and when severe enough, death (Shaw 1990). In northern England and Scotland, this cecal nematode can be devastating to Red Grouse (*L. lagopus scoticus*); individual birds have been reported to carry more than 30,000 worms, although loads of 1000–3000 are more usual in heavily infested areas, and 5000–6000 seem to be fatal (Potts et al. 1984). How strongly this parasite may influence, perhaps even control, the cyclic nature of economically important *L. lagopus* populations in the British Isles is highly controversial (Hudson and Dodson 1990, Cherfas 1990). It should be noted, however, that this nematode does not seriously infest *L. lagopus* throughout the species' range (e.g., Pulliainen 1976).

Other possible cecal functions.—Besides those already discussed, a few other cecal functions have been reported or suggested (McNab 1973).

Significant amounts of vitamins, especially some of the B complex and vitamin B_{12}, were shown to be present in ceca and are probably produced by microbial activity (Couch et al. 1950), but virtually all the work was conducted in chickens. Whether or not cecal vitamin production is important in wild birds is unstudied. Chickens were also believed to be incapable of absorbing vitamins directly through the cecal wall—they had to ingest their cecal droppings if they were to benefit from this vitamin synthesis. In view of recent work on transport efficiency across the cecal wall, this may have been an unwarranted assumption.

Although coprophagy is widespread in parent birds that pick up and swallow the nutrient-rich feces initially produced by their young, few species are known to be coprophagic of adult fecal material. Duke, however, has seen domestic turkeys that were being commercially raised outdoors competing vigorously for and eating cecal droppings (pers. comm.). Wetmore (1926:31) also noted that in an Elegant Crested Tinamou he had just collected "The dung of the adult birds is greenish in color and soft in consistency with a very offensive odor. The crop and alimentary tract of the [downy] chick taken was filled with what was unmistakably the ordure of the parent." From its description, this fecal material was almost surely cecal in origin. It may have served to inoculate the young with important micro-organisms for the uniquely complex ceca found in this species (Fig. 3). It could also have provided the chicks with some other necessary dietary component. Whatever the answer, the presence of cecal feces in the upper gastrointestinal tract of a bird was unusual enough for a long-experienced field biologist to record. In the future, coprophagy may be found to be important in inoculating the ceca of young birds in this, and perhaps other, species (Braun and Duke 1989).

The cecal "tonsil," a visible nodule of lymphoid tissue at the proximal end of chicken ceca, has longer villi than the adjacent tissue and may act as an immunological monitor of luminal contents. The cecal tonsil contains B and T cells and all three classes of the known avian immunoglobulins, IgG, IgM, and IgA (Lebacq-Verheyden et al. 1972, Bienenstock et al. 1973, Glick 1986). Antigen production has also been suggested as a function for glandular ceca and the small ceca that are composed primarily or entirely of lymphatic tissue. This suggestion was made even before the vital immunologic function of the cloacal bursa (bursa of Fabricius) was discovered (Glick et al. 1956). However, subsequent investigations into the avian immunological system have been almost entirely based on chickens, especially when their system was shown to have a strong functional analogy to that of humans (Porter and Parry 1976). Even

the proportions of immunoglobulins in chicken cecal tonsils are not well established: Lebacq-Verheyden et al. (1972, 1974) found a predominance of IgA over IgG, whereas Bienenstock et al. (1973) found just the opposite. Clearly, the immunological contribution of ceca to avian physiology has only partly been elucidated.

Topics on cecal functioning that need to be addressed were outlined by Braun and Duke (1989:127–128) in their concluding remarks after the First International Avian Cecal Symposium. In part, these involved aspects of cecal motility (which we are pursuing), volume and composition of cecal contents, relationships between cecal size and colonic motility and contents, lower gut adaptation after cecectomy, functional cecal differences among species and between adults vs immatures and males vs females of the same species, and cautions about techniques, particularly the potential problems in using domestic birds and insufficient cecal preconditioning before experiments begin. To those remarks, we add:

Although cecal types and sizes have been recorded for many species of birds, the majority remain unreported—gaps in our knowledge that could be filled if more morphologists working with specimens realized the need was there.

When intestinal ceca change their length and/or mass in response to dietary changes, how is that change accomplished? Histological studies are needed.

It will be particularly important for physiologists to explore the functions of ceca that are not of the intestinal type—for instance, how do the large glandular ceca of owls and other birds differ from what is known about the intestinal type? Approximately two-thirds of the birds of the world have small or vestigial ceca that consist mainly of lymph tissue. Because selection pressures have not eliminated these small lymphatic ceca, it is reasonable to assume they have a valuable function. Obst and Diamond (1989) have shown that at least one of these lymphatic types (in the Rock Dove) is capable of transport. Are these small ceca important to a bird's immunological system? Although lymphatic ceca have no obvious special structures like the "tonsils" of galliforms (Klem et al. 1983, 1984), cells in these small ceca may well have similar functions, especially in producing immunoglobulins.

ACKNOWLEDGMENTS

We are grateful to curatorial staff members of The Carnegie Museum of Natural History and The National Museum of Natural History, Smithsonian Institution, for permission to examine alcohol-preserved specimens in their care. We are also grateful to John McLelland for lending us his copy of D. R. Naik's thesis. We especially thank Janet G. Hinshaw of the Wilson Ornithological Society's Van Tyne Memorial Library, for supplying copies of ref-

erences, and Alice W. Cullu, who, as always, gave invaluable editorial assistance on the manuscript.

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Wilson Bull., 107(1), 1995, pp. 122–130

BIAS IN CHRISTMAS BIRD COUNTS FOR SPECIES THAT VISIT FEEDERS

Erica H. Dunn[1]

Abstract.—In 1990 and 1991, compilers for 137 Christmas Bird Count (CBC) sites recorded observations of home-based "feeder-watchers" separately from CBC totals. In 29 of 49 species, there were significant positive relationships between the proportion of CBC totals seen by feeder-watchers and an index of feeder-watching effort (feeder-h/party-h). The effect on CBC totals is usually small but can be substantial in some species at high levels of feeder-watching effort, inflating CBC totals to over 67% more than would be the case with no feeder-watching. In addition, 73% of species had higher proportions of CBC totals recorded at feeders at high latitudes (feeder-watching effort held constant). Large changes in feeder-watching effort over time could produce spurious trends in population indices, particularly in northern areas. Suggestions are given for exclusion or correction of CBC data with high feeder-watching effort, but the best long-term solution is to record birds seen by feeder-watchers separately from those reported by field parties in all CBC publications and data bases. *Received 24 Jan. 1994, accepted 22 Aug. 1994.*

Many Christmas Bird Counts (CBC's) have participants who stay at home to observe feeders over prolonged periods. In 1975, CBC data bases began to record the number of these "feeder-watchers" and their hours of effort, but the birds seen by them continue to be incorporated in CBC totals.

A study conducted in Ithaca, New York, indicated that feeder-watching effort could potentially introduce a bias in CBC's. Participants recorded the number of each species seen at feeders, whether by field parties passing them briefly or by feeder-watchers. Results showed that, in some species, feeder-watchers saw as many as seven times more birds per feeder observed than did field parties (Butcher and Dunn, Kingbird, in press). If feeder-watching effort is relatively low, and/or field parties see large numbers of feeder-visiting species away from feeders, the effects of feeder-watching on CBC totals is probably small. In other cases, however, increased feeder-watching effort could potentially inflate CBC totals even though population levels actually remain stable.

Feeder-watching effort may vary geographically, with northern regions likely having a higher proportion of feeder-watching effort relative to field effort. Simultaneously, a greater proportion of local wintering populations may visit feeders regularly in harsher than in warmer climates. Thus, any biases introduced in CBC totals by inclusion of feeder observations might be greater in northern regions than elsewhere.

This paper examines temporal and geographic patterns in feeder-watch-

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ing effort, and the magnitude of its effects on CBC totals. It also determines whether more birds are seen by feeder-watchers in northern areas even when observation effort is held constant.

METHODS

Data were extracted from *American Birds* for a sample of CBC's done in 1978 and 1991 to determine whether feeder-watching effort changed between those two years. Feeder effort (feeder-h/party-h) was recorded for all sites in three regions (defined in Table 1) which were pre-selected to give approximately equal sample sizes and to represent geographic areas with wide north-south and east-west distribution. One count with over 500 feeder-h was excluded, because that effort was known to have resulted from an active educational outreach program that might have overwhelmed results from other count sites.

To determine the proportion of CBC totals recorded by feeder-watching, all CBC compilers were asked by the National Audubon Society (starting in 1990) to report on a voluntary basis the numbers of each species seen by feeder-watchers. Data from 1990 and 1991 were analyzed for this paper. If a count compiler submitted data in both years, only the first was included for analysis. For each of the 137 remaining locations, data were extracted from *American Birds* for all 89 species known to visit 15% or more of feeders within their winter range (unpubl. data from Project FeederWatch, a continent-wide cooperative survey of bird feeders run by the Cornell Laboratory of Ornithology and the Long Point Bird Observatory). Some of these species were later dropped from analysis because they were reported on fewer than 10 counts in the study sample.

For each species in each count, the proportion of the "reported total" (number published in *American Birds*) that was seen at feeders by home-based observers was calculated and transformed for use in analyses (square root of arcsin transformation, after appropriate adjustment for proportions of 0 and 1; Snedecor and Cochran, Statistical Methods, Sixth Edition. Iowa State Univ. Press, 1967:327–328). The transformed value was the dependent variable in stepwise multiple regression with the following independent variables: index of feeder-watching effort (feeder-h/party-h), latitude, longitude, and second- and third-order terms for each of these three variables to allow for curvilinear fits. To avoid distortion caused by small samples and to limit results to common species within the main part of their winter range all counts with fewer than 10 individuals of a species in the reported totals were excluded from analysis.

To the extent that feeder-watching effort and latitude or longitude are correlated in the compiler-contributed sample, the regression analysis described above may confuse their effects on proportion of CBC totals recorded at feeders. A stepwise regression of feeder-watching effort on latitude, longitude, and their second- and third-order terms did show a significant relationship with latitude[2]; but r^2 was only 0.09. Thus, any confounding of latitudinal effects with distribution of feeder-watching effort should be low. Another approach to this potential problem was to force effort variables into the regressions described in the previous paragraph, before allowing stepwise entry of latitude and longitude. This was tried and gave results similar to those presented here, but fewer species could be analyzed because of sample size constraints.

Results of the regressions were used to calculate the expected proportion of CBC totals that would be seen at feeders with various levels of feeder-watching effort, at 40°N, 90°W (an arbitrarily chosen point in Illinois). In addition, proportions at feeders were calculated for latitudes 45°N and 35°N (with longitude held at 90°W), and at longitudes 80°W and 100°W (with latitude held at 40°N), in both cases with feeder-watching effort set at 0.25 feeder-h/party-h.

TABLE 1

MEDIAN (AND MEAN) CHRISTMAS BIRD COUNT EFFORT BY HOME-BASED FEEDER-WATCHERS, OVER TIME AND BY LATITUDE[a]

Region[b]	1978		1991
North	0.00 (0.15)	**	0.08 (0.29)
	NS		NS
Central	0.06 (0.15)	NS	0.09 (0.16)
	+		***
South	0.00 (0.07)	NS	0.00 (0.06)
All areas	0.01 (0.13)	NS	0.04 (0.17)

[a] Effort measured as feeder-h/party-h. Count was included only if it was done both in 1978 and 1991 and if N feeder-h <500 (see methods). Symbols indicate significance of Kruskal-Wallis test between medians to either side of the symbol: NS = $P > 0.05$, + = $0.005 < P < 0.10$, ** = $P < 0.01$, *** = $P < 0.001$.

[b] Regions and sample size: North = British Columbia, Alberta and Ontario (N = 62 CBC's), Central = Oregon and Pennsylvania (61), South = California south of 37°, North and South Carolina and Georgia (61).

RESULTS

Feeder-watching effort increased between 1978 and 1991 in northern areas and tended to be higher in the north as well (Table 1). Nonetheless, the majority of counts had relatively low levels of effort. The means in Table 1 are much higher than the medians because of highly skewed distribution of effort (solid line, Fig. 1). Five percent of the counts in 1991 had effort indices >1.0. The sample contributed by compilers was biased towards counts with high levels of effort (dashed line, Fig. 1).

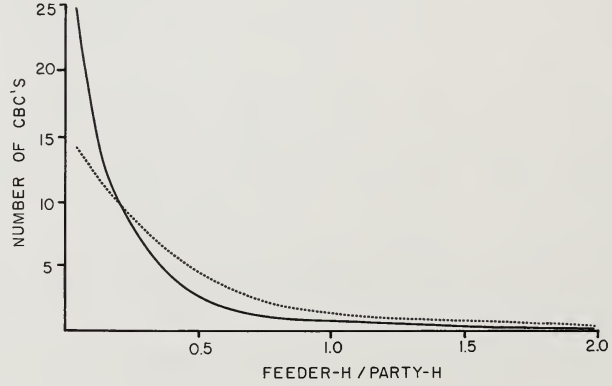

FIG. 1. Frequency distribution of Christmas Bird Counts according to effort expended on watching feeders. Solid line fit by eye to 1991 data from complete sample of feeders from defined areas (Table 1, N = 183); dashed line shows 1990–1991 data contributed to this study by count compilers (N = 137).

Median effort in the latter sample was 0.28 feeder-h/party-h, and 12% of cases had effort indices >1.0.

Analysis of the sample of CBC's contributed by compilers showed that the proportion of CBC totals seen at feeders depended significantly on feeder-watching effort in 29 (59%) of the 49 species analyzed (Table 2). The distorting effects of high feeder-watching effort on CBC totals can be substantial (Fig. 2). At an effort level of 0.1 party-h/feeder-h, only one species was predicted to have its CBC totals inflated by 10% or more above what they would have been without any feeder-watching effort. When feeder-watching effort rose to 0.25 feeder-h/party-h, however, 17% of species totals were inflated by >10%, and the number of affected species increased dramatically at still higher levels of feeder-watching effort (Fig. 2).

In 73% of species, higher proportions of CBC totals were seen at feeders at high latitudes (feeder-watching effort held constant). To illustrate the magnitude of this effect, the proportion of CBC totals seen at feeders that was expected at 45°N was divided by the expected proportion at 35°N (Fig. 3).

Longitude affected the proportion at feeders in fewer species (31%). A higher proportion of CBC totals was found at feeders in western areas in Downy Woodpecker, Black-capped Chickadee, Red-breasted Nuthatch, Common Raven, Eastern Bluebird, American Robin, Northern Mockingbird, House Sparrow, Cedar Waxwing, European Starling, Song Sparrow, White-crowned Sparrow and Common Grackle (scientific names in Table 2). Higher proportions were found in eastern areas in American Crow and Bohemian Waxwing.

DISCUSSION

Christmas Bird Count totals can be substantially inflated by high levels of feeder-watching relative to field party effort. Thus, if feeder-watching effort changes markedly over a period of years, spurious population trends could be produced.

These results have to be considered in the context of what is "normal." Over a broad geographic area, median feeder-watching effort was only 0.04 feeder-h/party-h in 1991 (Table 1). The maximum change in median values between 1978 and 1991 was in northern areas (from 0 to 0.08 feeder-h/party-h). These values were used to estimate the resultant degree of inflation expected in field party totals at an arbitrary latitude and longitude (see methods for calculation). CBC totals were predicted to rise by 1% in nine species (Hairy Woodpecker, Blue Jay, Black-capped and Carolina chickadees, Carolina Wren, Northern Cardinal, Dark-eyed Junco, House Sparrow and Pine Siskin), by 2% in two species (Downy Wood-

TABLE 2

SPECIES WITH EFFECTS OF FEEDER-WATCHING EFFORT ON CBC TOTALS[a]

Species (and 4-letter code)	Correction formula[b]
Ring-necked Pheasant (RNPH) (*Phasianus colchicus*)	$0.26E$
Rock Dove (RODO) (*Columba livia*)	$0.02E^3 + 0.19LAT$
Mourning Dove (MODO) (*Zenaida macroura*)	$0.28E + 2.96LAT^3$
Red-bellied Woodpecker (RBWO) (*Melanerpes carolinus*)	$0.29E + 3.23LAT^3$
Northern Flicker (NOFL) (*Colaptes auratus*)	$0.18E + 0.33LAT$
Downy Woodpecker (DOWO) (*Picoides pubescens*)	$0.82E - 0.54E^2 + 0.12E^3 + 1.72LAT^2 - 0.17LONG^2$
Hairy Woodpecker (HAWO) (*P. villosus*)	$0.37E - 0.04E^3 + 3.45LAT^3$
Blue Jay (BLJA) (*Cyanocitta cristata*)	$0.41E - 0.04E^3 + 1.12LAT^2$
American Crow (AMCR) (*Corvus brachyrhynchos*)	$0.11E + 0.65LAT^3 + 0.07LONG^3$
Common Raven (CORA) (*C. corax*)	$0.01E^3 + 0.10LONG$
Tufted titmouse (TUTI) (*Parus bicolor*)	$0.37E + 0.64LAT$
Black-capped Chickadee (BCCH) (*P. atricapillus*)	$0.17E + 1.88LAT^2 - 0.12LONG^3$
Carolina Chickadee (CACH) (*P. carolinensis*)	$0.66E + 0.27LAT$
White-breasted Nuthatch (WBNU) (*Sitta carolinensis*)	$1.13E - 0.93E^2 + 0.23E^3 + 0.88LAT^2$
Carolina Wren (CAWR) (*Thryothorus ludovicianus*)	$0.27E + 3.08LAT^3$
European Starling (EUST) (*Sturnus vulgaris*)	$0.12E + 0.07LONG$
Northern Cardinal (NOCA) (*Cardinalis cardinalis*)	$0.32E + 3.16LAT^3$
Song Sparrow (SOSP) (*Melospiza melodia*)	$0.10E^3 + 3.35LAT^3 - 0.10LONG^2$
American Tree Sparrow (ATSP) (*Spizella arborea*)	$0.03E^3 + 2.05LAT^3$
Field Sparrow (FISP) (*S. pusilla*)	$0.06E^2 + 0.19LAT$
Dark-eyed Junco (DEJU) (*Junco hyemalis*)	$0.26E + 1.27LAT^2$
Brewer's Blackbird (BRBL) (*Euphagus cyanocephalus*)	$0.11E^2 + 0.11LAT$
House Sparrow (HOSP) (*Passer domesticus*)	$0.45E - 0.13E^2 + 0.17LONG$

TABLE 2
CONTINUED

Species (and 4-letter code)	Correction formula[b]
Pine Siskin (PISI) (*Carduelis pinus*)	$0.21E + 0.40LAT$
American Goldfinch (AMGO) (*C. tristis*)	$1.12E - 0.88E^2 + 0.21E^3 + 0.88LAT^2$
Common Redpoll (CORE) (*C. flammea*)	$0.14E^2 + 0.25LAT$
Pine Grosbeak (PIGR) (*Pinicola enucleator*)	$0.25E$
Purple Finch (PUFI) (*Carpodacus purpureus*)	$0.43E + 0.73LAT$
House Finch (HOFI) (*C. mexicanus*)	$0.73E - 0.35E^2 + 1.47LAT^2$

[a] Species analyzed but with no effects of feeder-watching effort: Pileated Woodpecker (PIWO), (*Dryocopus pileatus*); Scrub Jay (SCJA), (*Aphelocoma coerulescens*); Black-billed Magpie (BBMA), (*Pica pica*); Brown Creeper (BRCR), (*Certhia americana*); Red-breasted Nuthatch (RBNU), (*S. canadensis*); Ruby-crowned Kinglet (RCKI), (*Regulus calendula*); Eastern Bluebird (EABL), (*Sialia sialis*); American Robin (AMRO), (*Turdus migratorius*); Northern Mockingbird (NOMO), (*Mimus polyglottos*); Bohemian Waxwing (BOWA), (*Bombycilla garrulus*); Cedar Waxwing (CEWA), (*B. cedrorum*); Yellow-rumped Warbler (YRWA), (*Dendroica coronata*); Rufous-sided Towhee (RSTO), (*Pipilo erythrophthalmus*); White-throated Sparrow (WTSP), (*Zonotrichia albicollis*); White-crowned Sparrow (WCSP), (*Z. leucophrys*); Eastern Meadowlark (EAME), (*Sturnella magna*); Red-winged Blackbird (RWBL), (*Agelaius phoeniceus*); Brown-headed Cowbird (BHCO), (*Molothrus ater*); Common Grackle (COGR), (*Quiscalus quiscula*); Evening Grosbeak (EVGR), (*Coccothraustes vespertinus*).

[b] To get the expected proportion of CBC reported totals seen by feeder-watchers (in CBC's with >10 individuals in the reported totals), square the sin of the value produced by the formula. E = feeder-h/party-h, LAT = latitude/100 and LONG = longitude/100 (where minutes are converted to tenths of degrees).

pecker and Purple Finch), and by 3% in three species (White-breasted Nuthatch, American Goldfinch, and House Finch).

Over a long period of years, inflation of CBC totals of this magnitude should have little effect on detection of important population trends. However, when the mean (instead of median) values for feeder-watching effort in northern areas (Table 1) were used in similar calculations, predicted inflation of CBC totals was as high as 5–7% in some species (Downy Woodpecker, White-breasted Nuthatch, American Goldfinch, and House Finch).

Clearly there is potential for strong bias in CBC reported totals for feeder species when feeder-watching effort is high. The simplest solution to ensuring that changing levels of feeder-watching do not contribute spuriously to population trends is to exclude from trend analysis any count that includes feeder-watchers. In certain analyses, however (e.g., those limited to northern states or provinces, or to species whose wintering range is primarily in northern areas), excluding counts with high feeder-watching effort may leave sample sizes too small for analysis. In

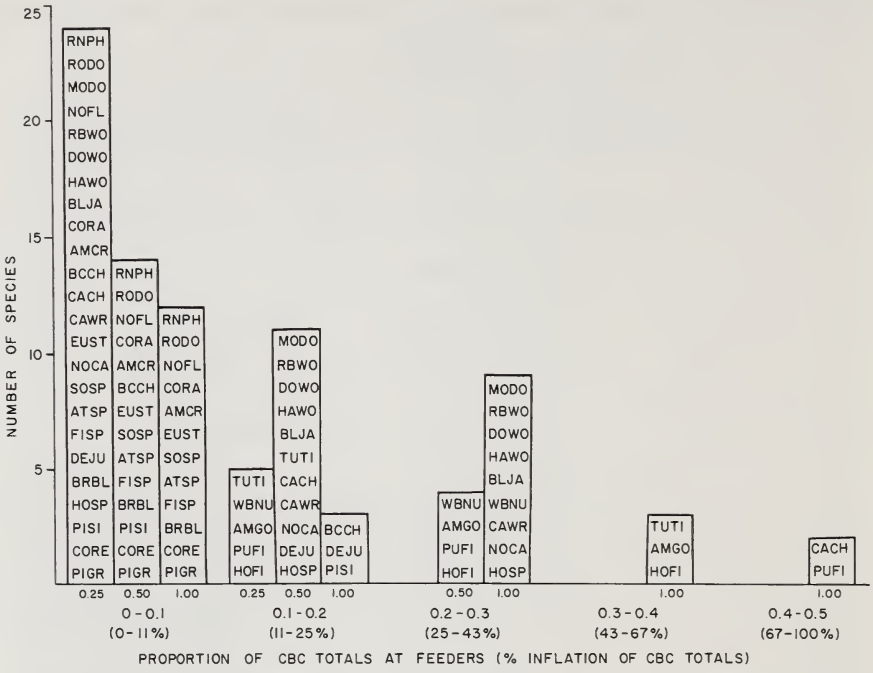

FIG. 2. Predicted proportion of CBC totals recorded at feeders at various levels of feeder-watching effort (feeder-h/party-h shown in small number under each bar). Numbers in parentheses indicate percent by which CBC totals are inflated over expected field totals. See Table 2 for key to four-letter species codes.

such cases, inclusion of counts with feeder-watching effort up to 0.05 or 0.10 feeder-h/party-h should limit inflation to modest levels (Fig. 2). Some counts with higher effort levels might also be included, if feeder-watching effort is more-or-less constant over the time period being investigated.

A limit of 0.1 feeder-h/party-h would still allow analysis to include 64% of the CBC's in the sample extracted from *American Birds* (Table 1) but only 22% of the compiler-contributed sample. In some cases, then, sample size is likely to be an issue, and the investigator will want to include CBC's with higher feeder-watching effort. Estimates of field-party totals alone could be derived from the regression results of this paper (Table 2). This is not recommended as a routine procedure, however, as application of these correction factors to years past is not entirely appropriate. Higher proportions of birds visit feeders in certain areas regardless of feeder-watching effort (e.g., Fig. 3), and the correc-

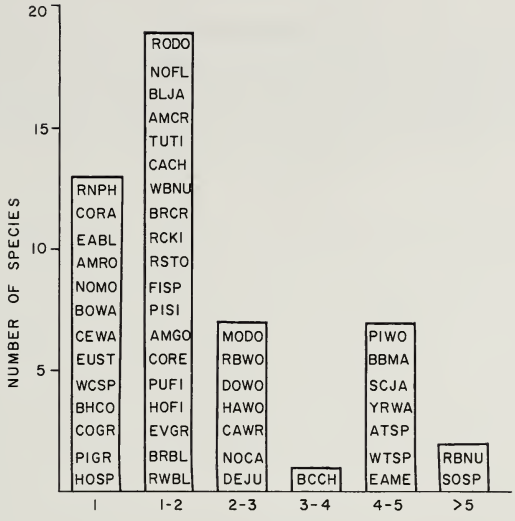

FIG. 3. Effect of latitude on proportion of CBC totals recorded at feeders when feeder-watching effort is held constant. X-axis shows number of times higher this proportion is at 45°N than at 35°N (see text). See Table 2 for key to four-letter species codes.

tion formulae are derived from 1990–1991 data that may have quite different geographic distribution of effort than in the past (see Table 1).

The most effective long-term solution to the problem of bias in CBC's due to inclusion of feeder counts is for observations of home-based participants to be kept separate from those of field parties in all CBC publications and data bases (Butcher and Dunn, in press). This would circumvent any pitfalls associated with the analysis solutions suggested here. An added benefit would be the documentation of any geographic, temporal, or weather-related patterns in numbers of birds visiting feeders compared to their numbers "in the wild."

There probably is another bias remaining in CBC's for feeder species, even after removal of the effects of home-based feeder-watching. Birds visiting feeders may be more visible to field parties than birds elsewhere, and the booming post-war hobby of bird-feeding could have led to increased "countability" of feeder species in the field (Butcher and Dunn, in press). The problem is likely to be most severe in northern areas, based on evidence that higher proportions of wintering populations visit feeders at high latitudes (Fig. 3). The magnitude of this problem is unknown, however, and can be handled only through caution in interpretation of population trends for feeder species that are derived from CBC data, even when home-based observations have been accounted for.

ACKNOWLEDGMENTS

Geoff LeBaron and Susan Drennan of the National Audubon Society gave permission to approach CBC compilers for data and took care of all mailings. Greg Butcher helped get the data-collection underway. The count compilers who contributed data deserve special thanks.

Wilson Bull., 107(1), 1995, pp. 131–139

NON-MIGRATORY MOVEMENTS OF DUNLINS ON THEIR CALIFORNIA WINTERING GROUNDS

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Abstract.—In 1991–1992, we tracked 150 marked Dunlins (*Calidris alpina*) from two central California coastal sites to ascertain if they made winter-time movements to inland areas and examined census data from these and other coastal sites to document the possible extent and frequency of these movements. Between December 1991 and January 1992, Dunlin numbers at four central California coastal sites decreased by 44–84% during periods of heavy rain. Subsequently, six or seven of the marked Dunlins from one of these sites were located inland, up to 140 km away. The sudden disappearance of more than 40% of the wintering Dunlins from this coastal area in 10 of 21 years suggests that such movements may be fairly frequent. Median (October–March) numbers of Dunlins at this site during the 21 years were negatively correlated with local rainfall, suggesting a relationship between winter storm activity and the level of use of coastal sites. It remains to be determined whether deteriorating conditions in coastal wetlands or the increased availability of inland habitats related to winter storms is responsible for reducing Dunlin winter-time use of coastal sites. *Received 28 March 1994, accepted 6 Sept. 1994.*

Although much has been learned about the distribution and abundance of shorebirds in the Pacific Flyway in recent years (Page et al. 1992), how different sectors of the flyway are linked together remains poorly understood, particularly for wintering shorebirds. Small scale movements of shorebirds are known to occur in winter, often in response to specific weather conditions. Eurasian Curlews (*Numenius arquata*) move between coastal mudflats and agricultural fields up to 30 km away, depending on weather (Bainbridge and Minton 1978, Townshend 1981) and perhaps moon phase (Hale 1980). Freezing weather in Europe forces Lapwings (*Vanellus vanellus*) and Greater Golden-Plovers (*Pluvialis apricaria*) from inland fields to coastal estuaries (Hale 1980). Local movements of 2–10 km between estuaries and fields in response to rain, snow, or ice have been documented for Redshanks (*Tringa totanus*), Dunlins (*Calidris alpina*), Black-bellied Plovers (*Pluvialis squatarola*), Killdeers (*Charadrius vociferus*), Marbled Godwits (*Limosa fedoa*), Least Sandpipers (*Calidris minutilla*), Western Sandpipers (*C. mauri*), Greater Yellowlegs (*Tringa melanoleuca*), and dowitchers (*Limnodromus* spp.) (Goss-Custard 1969, Hoff 1979, Page et al. 1979, Shuford et al. 1989, Ruiz et al. 1989).

Movements of greater distances have also been reported for some shore-

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birds. Wintering Red-necked Stints (*Calidris ruficollis*) respond to newly-flooded inland habitat by moving from the coast to the interior of eastern Australia; in contrast, droughts force Red-kneed Dotterels (*Erythrogonys cinctus*), Black-winged Stilts (*Himantopus himantopus*), Banded Stilts (*Cladorhynchus leucocephalus*) and Red-necked Avocets (*Recurvirostra novaehollandiae*) from interior breeding sites to coastal wetlands (Lane 1987). In South Africa, Greenshanks (*Tringa nebularia*) move to the coast after summer rains inundate their interior sites (Tree 1979).

It has been speculated that wintering Dunlins in California move inland from coastal sites in response to storms and high tides (Strauch 1967, Page 1974, Page et al. 1979, Ruiz et al. 1989, Shuford et al. 1989), but this has not been confirmed through direct observations. From December 1991 to March 1992, we tracked marked Dunlins from two central California coastal sites for evidence of movements inland during winter. We also examined census data from four coastal sites to document the possible extent and frequency of these movements.

STUDY AREAS AND METHODS

Each year, between October and March, up to 5000 Dunlins reside at the 587-ha Bolinas Lagoon, Marin County (Shuford et al. 1989), and up to 6000 at the 320-ha Bodega Harbor, Sonoma County, California (Ruiz et al. 1989), about 50 km away (Fig. 1). From 12 December 1991 to 27 January 1992, we trapped 150 Dunlins in mist nets at Bolinas Lagoon and Bodega Harbor. Twenty-five birds were captured at Bodega between 8–16 January, marked ventrally with a solution of picric acid and a green plastic color band was applied on the upper leg. At Bolinas, 51 Dunlins captured from 12 December to 7 January were marked similarly, except for red color bands; 64 additional Dunlin were marked individually with four color bands but not dyed. Another 10 birds, captured at Bolinas from 7–27 January were fitted with 1-g radio transmitters, having a range of approximately 2 km from the ground and 4–7 km from the air. Radio battery life was about seven weeks (Warnock and Warnock 1993).

Bolinas Lagoon was checked for marked birds almost daily from 12 December 1991 to 28 February 1992. We searched Richardson Bay, within central San Francisco Bay (Fig. 1), on 29 dates between 17 January and 25 February after we received reports of dyed birds being present there. Other accessible regions of north and central San Francisco Bay were also checked four times during this period. On 28 February, we searched for the radio signals of marked birds from an aircraft throughout north San Francisco and Suisun bays. On four dates from 13 February to 6 March, parts of the Sacramento Valley were monitored for radio-tagged birds by an observer in an automobile and, on 20 and 26 February, aerial searches for radio-tagged birds were conducted in the Sacramento-San Joaquin River Delta and the Sacramento Valley north to the Sutter Buttes (Fig. 1). On 27 February, we checked for dyed and radio-tagged Dunlins in many of the wetlands accessible by road in the northern San Joaquin Valley (Fig. 1) and scanned for radio-tagged birds from a 20-m tower located near the center of the upper San Joaquin Valley. Newsletter notices were also used to alert bird watchers and duck hunters to look for dyed Dunlins.

To examine the extent and frequency of large scale departures of Dunlins from the coast, we examined shorebird censuses taken weekly to monthly from October through March at

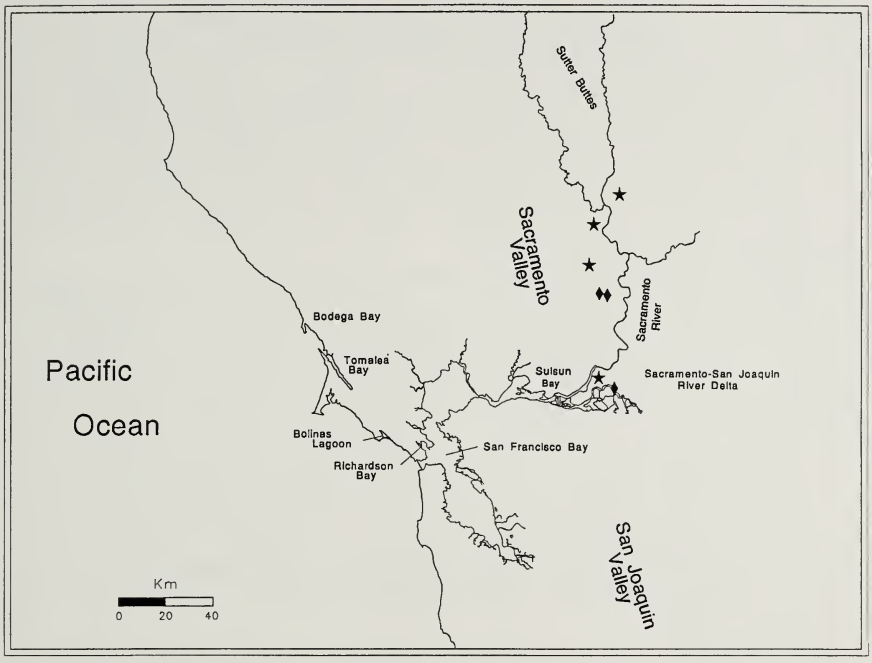

FIG. 1. Map showing study sites as well as resighting locations away from Bolinas Lagoon of radio-tagged (★) and dyed/color-banded (♦) Dunlin.

Bolinas Lagoon between 1971 and 1992, and monthly at Bodega Harbor, Tomales Bay, and San Francisco Bay (16 sites) between October 1991 and March 1992. All counts at Bolinas Lagoon were accomplished by three teams of observers covering their respective areas simultaneously; censuses were generally timed so that the rising tide would be about 1.4 m above mean low water by mid-count. Marked departures of Dunlins at Bolinas Lagoon were defined as any decline of 40% or more between mean monthly numbers that was not counteracted by a notable increase in the following months.

We also examined the residency patterns of 75 individually marked Dunlins that were present at Bolinas Lagoon in at least three of the four years from 1984–1987. The length of stay of these individuals was available from extensive observations ($\bar{x}$ = 89.5 days of sightings, range 73–111 days from 30 Sept.–15 April) during four consecutive seasons. Other years could not be used because we lacked complete coverage over the period that Dunlins were present.

To test whether Dunlin numbers at Bolinas Lagoon varied with amount of local rainfall, we regressed the natural log-transformed median number of Dunlins at Bolinas Lagoon between 24 Oct. and 31 Dec. against the mean amount of rainfall at Bolinas from October through December for the 21 year period from 1971 to 1991.

RESULTS

Dunlins dyed at Bolinas Lagoon in 1991 were first located 14 km away in San Francisco Bay (at Richardson Bay) on 28 December 1991. Sub-

sequently, up to five dyed Dunlins were seen in Richardson Bay through January. Nine of the 10 radio-tagged Dunlins also travelled at least once to Richardson Bay then back to Bolinas (median number of moves = 3, range = 1–8 moves). Seven moved from Bolinas to Richardson Bay and then back to Bolinas within one 12-hr period. On three occasions, birds were recorded at Bolinas and then in Richardson Bay less than one hour later (range = 38–57 min.). No dyed Dunlins from Bodega were sighted in San Francisco Bay or elsewhere.

Four radio-tagged Dunlins were located in the Sacramento-San Joaquin River Delta or the Sacramento Valley, up to 140 km from Bolinas (Fig. 1). One, last seen in Bolinas on 10 February, was found in the delta on three dates between 18–26 February. The other three, last seen at Bolinas or Richardson Bay between 10–14 February, were located in the Sacramento Valley on both 20 and 26 February. None of the four birds was recorded at Bolinas Lagoon or Richardson Bay later in the spring of 1992, but two returned to Bolinas in the fall of 1992. One color-banded Dunlin from Bolinas was sighted in the delta on 25 February, and two dyed Dunlins (one positively from Bolinas) were seen in the Sacramento Valley on 22 and 25 February (Fig. 1). No marked Dunlins were found in the San Joaquin Valley.

Dunlin numbers at Bolinas Lagoon and three other central California coastal sites fell steeply between December 1991 and January 1992 (Fig. 2). Numbers declined by 66% at Bolinas Lagoon, 84% at Bodega Harbor, 64% at Tomales Bay, and 44% at San Francisco Bay. Numbers at Bolinas declined by a further 89% from January to February 1992 (Table 1).

Winter-time departures of 40% or more of the Dunlin from Bolinas Lagoon were noted on 13 occasions in 10 of 21 seasons between 1971–1991 (Table 1). The declines occurred from November to December once, December to January five times, and January to February seven times (Table 1). There were no marked departures during 10 years, and in 1984, numbers fell by over 50% between November and December but subsequently rose again. The average number of Dunlin in the month prior to departures ranged from 1100 to 4821 birds ($\bar{x}$ = 2693, SD = 2693, N = 10). The mean November–February numbers (each month given equal weighting) during the 10 years without marked departures ranged from 1041 to 4306 birds ($\bar{x}$ = 2327, SD = 989).

Individually-marked Dunlins differed in their residency patterns at Bolinas Lagoon through the four years that were examined. Thirty-nine percent (N = 75) that consistently arrived in the fall and departed in the spring did not abandon their coastal wintering site during any of three periods of large scale departures at Bolinas Lagoon. In contrast, 26% consistently disappeared during departure periods and 9% left during two

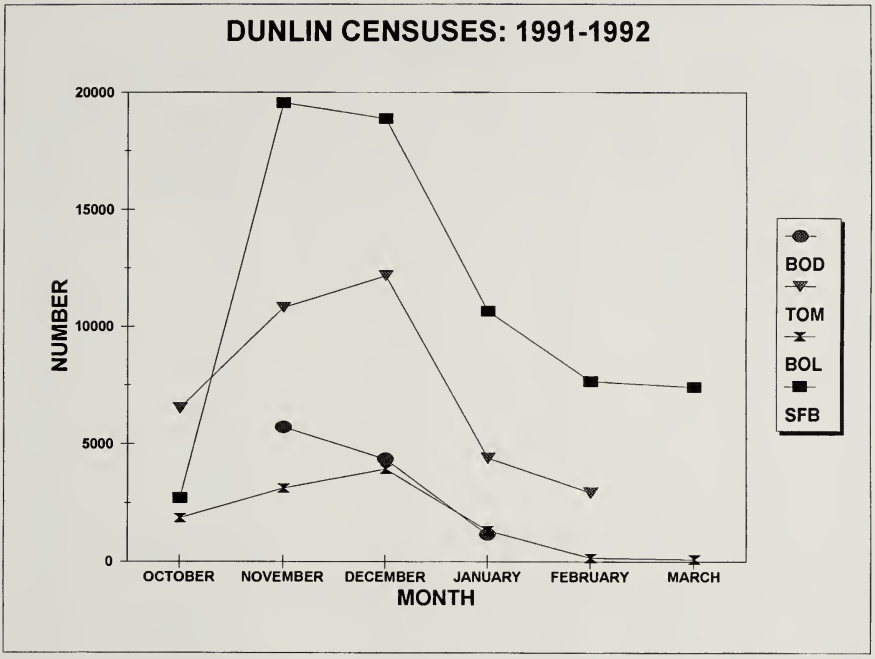

FIG. 2. Numbers of Dunlins counted in monthly censuses at Bodega Bay (BOD), Tomales Bay (TOM), Bolinas Lagoon (BOL), and San Francisco Bay (SFB) in 1991–1992.

but remained through one departure period. Of the remaining birds, 7% consistently arrived and departed prior to departure periods and 19% had patterns that were ambiguous with regard to the departures.

Over 21 years, median yearly (October–March) numbers of Dunlins at Bolinas Lagoon were significantly negatively correlated with local fall rainfall ($r^2 = 0.66$, $P < 0.001$).

DISCUSSION

This study confirms that some Dunlins in central California move inland from the coast during some winters. The rapid disappearance of more than 40% of the wintering Dunlins from Bolinas Lagoon in 10 of 21 years suggests that such movements may be fairly frequent. Abandonment of coastal wetlands for inland habitats is probably not restricted to Bolinas Lagoon or the central California coast, since there was a winter decline in the numbers of Dunlins at three other wetlands on the central coast in 1991–1992; Mark Colwell (pers. comm.) reported the departure of Dunlins from Humboldt Bay on the north coast of California during the same period.

TABLE 1
MEAN MONTHLY NUMBERS OF DUNLIN AT BOLINAS LAGOON DURING 21 SEASONS

	October	November	December	January	February	March
1971	2502	3666	3124	1718 (45%)[a]	1339	1089
1972	2092	1912	1705	887 (48%)	243 (83%)	289
1973	1327	1353	1004	879	926	862
1974	2019	3837	3092	2513	2019	2035
1975	2763	4581	4295	4237	4110	4060
1976	1812	2394	3058	3795	3446	5084
1977	2236	2211	2067	1455	2186	2614
1978	1092	2641	2148	1974	2724	1816
1979	487	1915	1969	2439	2390	1931
1980	34	2391	3028	2623	2598	1253
1981	278	1797	1388	1246	1581	37
1982	1940	2144	343 (84%)	960	940	725
1983	1892	1185	—	1285	1109	992
1984	1000	900	245	600	1032	1048
1985	1985	1576	1202	1100	587 (47%)	520
1986	2356	1775	2853	2917	1356 (54%)	691
1987	1669	3115	2092	1184 (54%)	987	539
1988	3276	1897	2469	1132 (54%)	680 (40%)	60
1989	2275	3020	2951	3021	1713 (43%)	1823
1990	4338	3734	5845	4821	755 (84%)	34
1991	1869	3131	3931	1321 (66%)	151 (89%)	95

[a] (% N) = Percent decline of Dunlin population from previous month; only declines ≥40% shown.

The first documented winter exodus of large numbers of Dunlins from Bolinas Lagoon in 1972–1973 coincided with a period of heavy rainfall (Page 1974, Page et al. 1979, Shuford et al. 1989). The 1991–1992 departure, which involved radio-tagged and dyed birds, also occurred during a period of heavy rainfall. Observations such as these and a negative correlation between winter numbers at Bolinas and amount of local rainfall suggest movement inland from the coast may be related to winter storms, but the nature of this relationship is not clear. The negative correlation between rainfall and numbers of wintering Dunlin could also reflect, in part, differences in the number of birds settling at Bolinas Lagoon relative to amount of rainfall.

Winter storms may cause feeding conditions for Dunlins to deteriorate in coastal wetlands. Winter months can be harsh for shorebirds at Bolinas Lagoon due to a general decrease in invertebrate prey items, increased numbers of potential competitors, and decreased daylight exposure of tidal flats (Stenzel et al. 1983). Winter storms cause a further deterioration of feeding conditions. Associated with the storms are increased runoff,

strong southerly winds, and low air pressure, all of which cause water levels to remain higher than normal and result in less feeding time for Dunlins. Rain is also known to affect negatively feeding and capture rates of some shorebirds in tidal areas (Goss-Custard 1970, 1984; Pienkowski 1981). At Bolinas Lagoon, Dunlins have been observed to switch from feeding on invertebrates to small fish (*Clevelandia ios*) during heavy rainfall (Warnock 1989), but the cost or benefit of this change is unknown.

Dunlins may also abandon the coast in response to increased availability of inland habitat in the Sacramento Valley where 162,000 ha of agricultural lands are subject to flooding from river overflows and local runoff during wet winters and 32,000 ha of harvested rice fields are intentionally flooded for waterfowl hunting during fall and winter (Heitmeyer et al. 1989). In the San Joaquin Valley, about 50,000 ha of wetlands are seasonally flooded during winter rains (Heitmeyer et al. 1989). Thus several interacting factors may cause wintering Dunlins to abandon Bolinas Lagoon for the interior or cause them not to settle there at all.

The function of the local Dunlin movements between Bolinas Lagoon and San Francisco Bay is unclear. The 50-min difference in high tides seems too short to provide much opportunity for Dunlin to exploit the tidal time lag between sites. Differences in food resources could account for the local movements as has been suggested for Dunlins within San Francisco Bay (Holway 1990). Return movements back to Bolinas Lagoon could be prompted by heavy human disturbances of the limited roost sites in Richardson Bay (Warnock, pers. obs.). The flights could also be scouting trips to assess conditions outside of Bolinas Lagoon. All four radio-tagged Dunlins, found in the Sacramento Valley, made at least one trip to San Francisco Bay within five days of departing from the Bay area.

Currently, little is known about why some shorebirds remain at one wintering site throughout a season while others depart. Most Grey (Black-bellied) Plovers in England spend the entire winter at one site every year, but a smaller number show up each year and then move on (Townshend 1985). The predominate pattern for Dunlins at Bolinas was to stay all winter, although some consistently participated in large scale departures. Townshend (1981) found that short-billed, male Eurasian Curlews were more likely to leave the coast and feed in fields than longer-billed females. He suggested that during cold weather these males were unable to reach marine invertebrates that burrowed deeper to escape the cold. An analogous situation might occur with Dunlins, since all of the known-sex birds participating in large scale movements in 1985, 1986 and 1987 were males, which average shorter bill lengths than females.

We have demonstrated that Dunlins in California will move from coast-

al to inland sites in winter. We have also shown that individual Dunlins have differing but often consistent patterns of seasonal movements. Research elucidating the mechanisms controlling these movements should lead to a better understanding of the interplay of coastal and interior wetlands in providing habitat for wintering shorebirds and lead to a more comprehensive conservation strategy for west coast shorebirds.

ACKNOWLEDGMENTS

Numerous individuals helped with the capture and resighting of color-banded Dunlins, in particular L. Arnow, B. A. Bateson, A. Brody, P. Hark, B. Kus, C. Shaw, J. Swenson, and J. Young. The Bolinas Lagoon census team is to be congratulated for censusing of shorebirds at Bolinas Lagoon for 21 years. Census results from other locations were provided by J. Kelly (Tomales Bay), P. Connors and J. Maron (Bodega Bay). Financial and logistic support to NW was provided by San Diego State University and the University of California, Davis. B. Collier, G. Cox, B. Kus, D. Van Vuren, and D. Anderson provided guidance for the study. Radiotelemetry work in the Central Valley was facilitated by J. Day and J. Takekawa of the Dixon office of the USFWS–Northern Prairie Wildlife Research Center. P. Moreno helped with radiotelemetry problems and GIS programs. M. Greene generously provided logistical support. Comments by M. Colwell, R. McNeil, S. McWilliams, and M. Pienkowski improved earlier versions of this manuscript. We are particularly grateful to S. Griffin-Warnock for her valuable insight and assistance in all phases of this study.

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Wilson Bull., 107(1), 1995, pp. 140–152

INVESTIGATOR DISTURBANCE, CHICK MOVEMENT, AND AGGRESSIVE BEHAVIOR IN RING-BILLED GULLS

KEVIN M. BROWN[1,2] AND RALPH D. MORRIS[1]

ABSTRACT.—Infanticidal attacks on conspecific young can be a major cause of chick mortality in ground nesting colonial seabirds, and past studies have shown that investigator disturbance scatters chicks, subjecting them to attacks by neighbors. In 1991, we studied the effects of investigator disturbance on aggressive behavior and chick movement at a Ring-billed Gull (*Larus delawarensis*) colony near Port Colborne, Ontario. The frequency of charges, jabs, and wingpulls increased during the period of investigator activity in the colony, while the duration of wingpulls and beakpulls decreased. Few chicks (<5%) less than seven days of age strayed from their natal territories during disturbances; most chicks (≥85%) remained crouched on the natal territory. However, chick mobility increased with age, and older (>7days) chicks strayed off their natal territories and were attacked more frequently during disturbances than before disturbance. In contrast to Fetterolf (1983; Wilson Bull. 95:23–41) who found that investigator disturbance increased chick mortality and decreased fledging success, in our study, no chicks were fatally attacked during investigator disturbance and stray chicks returned to their natal territories quickly after disturbance. Furthermore, the mean (± 1 SD) fledging success of pairs disturbed during this study (1.5 ± 0.8 chicks per pair) was not different from that recorded for undisturbed pairs (1.6 ± 0.8). As our results vary somewhat from Fetterolf's, we contrast the two sets of data in the context of experimental procedures that yielded them. In this study, suitable hiding places and termination of investigator visits into the colony after the hatching period were attributed to preventing human-induced chick mortality. We show that awareness of and attention to the potential impacts of investigator activity can reduce and even eliminate the negative consequences associated with such activity. *Received 14 March 1994, accepted 22 Aug. 1994.*

Infanticide and non-fatal attacks on conspecific young are commonly reported in ground nesting seabirds, especially gulls (Hunt and Hunt 1975, Davis and Dunn 1976, Fetterolf 1983a, Pierotti and Murphy 1987, Pierotti 1991). Infanticide can be an important cause of chick mortality. Pierotti (1982) observed that 92 percent of Herring Gull (*Larus argentatus*) chick mortality at one site on Great Island, Newfoundland, was attributable to attacks by neighbors. This high level of infanticide was attributed to small territory size, and a few deaths were a result of investigator disturbance (Pierotti, pers. comm.). Similarly, Hunt and Hunt (1976) found that attacks by Glaucous-winged Gulls (*L. glaucescens*) accounted for at least 49 percent of the observed chick mortality. However, at other colonies, and other sites within colonies, infanticide is less frequent. At an adjacent

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site on Great Island, Pierotti (1982) observed that 92 of 95 dead Herring Gull chicks were killed by predatory Great Black-backed Gulls (*L. marinus*), while Graves and Whiten (1980) observed that only three of 27 attacks on trespassing Herring Gull chicks were fatal. Butler and Butler (1982), and Fetterolf (1984) found that chick survival was negatively correlated with aggression in Great Black-backed and Ring-billed gulls (*L. delawarensis*), respectively.

Although colonial seabirds are ideal for studies related to breeding success and behavior, chicks scatter into territories of neighboring pairs in response to human (investigator or other) disturbance and are frequently attacked (Robert and Ralph 1975, Anderson and Keith 1980, Safina and Burger 1983, Schoen and Morris 1984). Fetterolf (1983b) observed that infanticide in Ring-billed Gulls was rare under natural conditions; three of 1100 chicks (<0.3%) were killed by conspecific attacks at undisturbed colony sites. He suggested that human-induced chick mortality in past studies may have confounded theoretical interpretations of reproductive strategies involving terrestrial nesting colonial seabirds.

However, numerous other factors have also been shown to influence chick movement and aggression by adjacent adults, including the extent of nest cover, nesting density (Hunt and Hunt 1976, Fetterolf 1984, Pierotti and Bellrose 1986, Pierotti 1987, Watanuki 1988), and nesting synchrony (Fetterolf 1984, Reville 1988). Watanuki (1988) also found that the rate of cannibalism varied among three colonies of Slaty-backed Gulls (*L. schistisagus*) and may reflect differences in food supply and predatory habits. Furthermore, investigators usually design their experimental protocols and visitation schedules in order to minimize disturbance effects by terminating visits into seabird colonies once chicks become mobile (Parsons 1972, Fetterolf 1984, Hébert and Barclay 1986, Morris and Siderius 1990). The purpose of this paper is to report the influence of disturbance caused by our activities in a Ring-billed Gull colony on (1) the frequency and duration of aggressive behaviors by adults towards neighboring adults and chicks and (2) chick movement and behavior. Our results are contrasted with those reported by Fetterolf (1983b).

STUDY AREA AND METHODS

The study site was an artificial breakwall located 1 km off the north shore of Lake Erie and 1 km west of the Welland Ship Canal near Port Colborne, Ont (42°53′N, 79°16′W). Approximately 2500 pairs of Ring-billed Gulls and 150 pairs of Herring Gulls nested on a limestone rockpile adjacent to the west arm of the breakwall. On 2 April 1991, prior to egg laying, a study area (7 × 7 m) was marked and an observation blind erected 2–3 m from one edge of the study plot which allowed for maximum visibility of study area. Nest density was subsequently 1.2 nests/m^2.

The study area was visited daily during the egg-laying, incubation and hatching periods.

The colony was not entered during mid-day or rainy periods. Activities performed by an assistant on each visit included (1) marking new nests, (2) numbering, measuring, and weighing eggs, and (3) individually marking chicks. All chicks from peak clutches were dyed with Rhomadine B with respect to hatch order: a-chicks (first hatched) on the head, b-chicks (second hatched) on the breast, and c-chicks (third hatched) on the rump. In addition, chicks from twelve 3-chick broods were uniquely color-banded. In these twelve broods, a- and b-chicks hatched on the same day and c-chicks hatched up to 48 h later. Visits to the colony lasted 30–60 min and were terminated 31 May following the hatching of all eggs from peak 3-egg clutches. Every attempt was made to minimize disturbance effects. For example, we restrained chicks that attempted to run by covering them with a hand until they crouched, or we placed them in nearby cover while working in the immediate vicinity (see Rodgers and Burger 1981).

Data regarding the influence of investigator disturbance on adult and chick interactions were recorded from a blind by continuous scan sampling 30 min prior to, 30 min during, and for two consecutive 30-min periods after investigator disturbance by an assistant (hereafter referred to as before, during, after and after(2) disturbance, respectively). As peak feeding and other activities in Ring-billed Gull colonies usually occurs two to four hours following sunrise and prior to sunset (Haymes and Blokpoel 1978, Kirkham and Morris 1979), most observation periods began between 06:00 and 08:00 (N = 18), three prior to 10:00, and four prior to 12:00 EST.

Adult–adult interactions.—The frequencies of adult–adult aggressive interactions were recorded from 23 April to 29 May (N = 23 days) including charges, jabs, wing pulling, beak pulling, and fighting (two or more jabs exchanged by two adults). In addition, the duration of beakpulls and wingpulls during each time period was timed using a stop watch and recorded (secs).

On 2, 3, and 4 May, two investigators simultaneously recorded the frequency of aggressive acts in order to standardize the recording of behavior categories. On 10 May, the two observers independently and simultaneously recorded the frequencies of aggressive interactions at five-min intervals for 2 h to determine reliability of category recording.

Chick movement and adult–chick interactions.—Chick movement and adult–chick interactions were recorded daily throughout the hatching period (15–31 May 1991). Chick movement data included whether a chick was straying from or returning to its natal territory and age and brood rank of the mobile chick. Adult–chick interactions included the number and identity of chicks attacked, the number of adults attacking each chick, the number of pecks delivered per attack, the number of 'chick-shakes' (adult grasps and shakes chick), and location of chick attacks (on or off their natal territories). The physical condition (e.g., head lacerations, damaged limbs) of chicks was also recorded.

Chick behavior.—The behavior of 36 leg-banded chicks was recorded by point-sampling at two 15-min intervals before, during, and after disturbance on six days between 25–31 May. Chick behaviors were grouped into four categories: active on territory, inactive on territory, active off territory, and inactive off territory. Active chicks were standing, wandering, begging, or being fed. Inactive chicks were hiding, crouching, or being brooded. Chicks not observed at the time of point sampling were not included.

Frequency data were analyzed using several non-parametric statistical tests including Freidman rank tests, Wilcoxon sign-rank tests, Kruskal Wallace ANOVAs, and Mann-Whitney *U*-tests.

RESULTS

Reliability.—Nest density in the study area was high (1.2 nests/m^2), and aggressive interactions relatively frequent. Accordingly, to control for

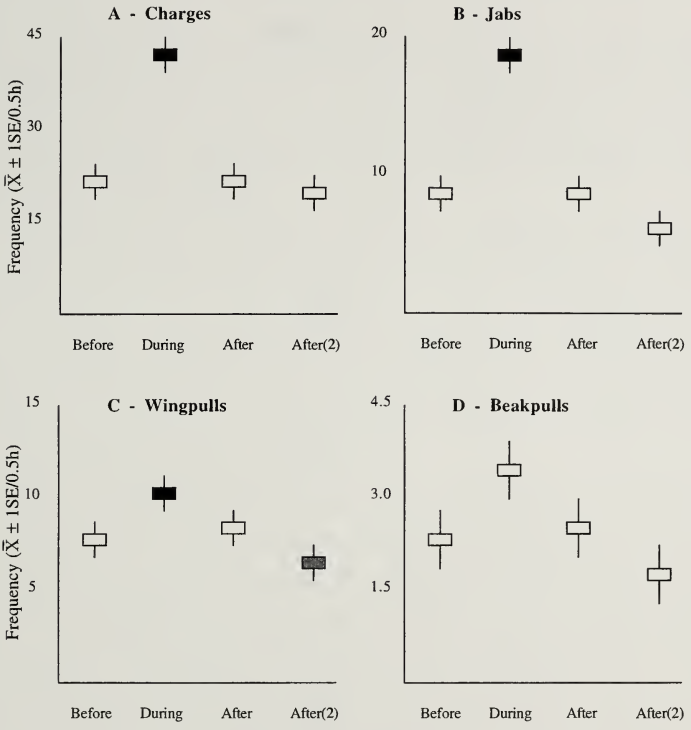

FIG. 1. The frequencies ($\bar{x}$ ± 1 SE/0.5 h, N = 23 per sampling category) of Ring-billed Gull aggressive interactions before, during, and two consecutive 0.5 h periods after (After and After2) investigator disturbance. A. Charges. B. Jabs. C. Wingpulls. D. Beakpulls. Different shades denote significance ($P < 0.05$) except wingpulls before vs after(2) ($P = 0.08$).

potential recorder error, adult behavior data were simultaneously collected by two independent observers at 5-min intervals over a 2 h period 10 May 1991. The Pearson correlation coefficient between observer one and observer two was 0.97, and $r^2 = 0.94$. Reliability was high; only 6% of the variation in the observed frequency of total aggressive interactions was due to error.

Adult–adult aggressive interactions.—The frequencies ($\bar{x}$ = 1 SD) of charges, jabs, wingpulls, and beakpulls before, during and after investigator disturbance are shown in Fig. 1. There were significant differences in the frequencies of charges (Freidman rank test: $\chi^2 = 30.3$, df = 3, $P = 0.01$), jabs ($\chi^2 = 43.0$, df = 3, $P = 0.01$) and wingpulls ($\chi^2 = 15.8$, df = 3, $P = 0.01$) among the four sampling periods. Pairwise comparisons revealed that the frequencies of charges, jabs, and wingpulls were all significantly higher during disturbance than before disturbance and for

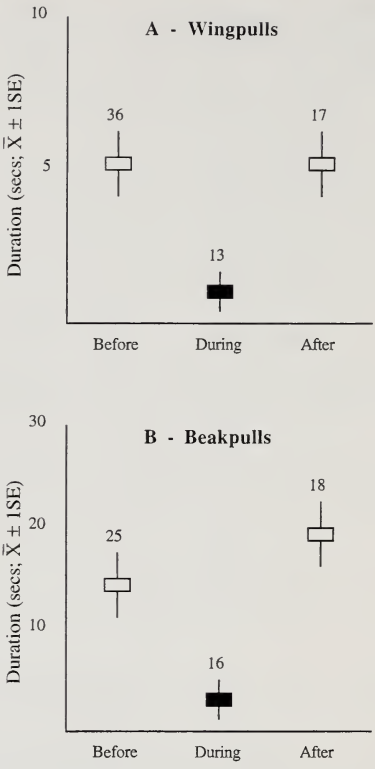

FIG. 2. The mean duration (secs; ± 1 SE) of wingpulls (A) and beakpulls (B) before, during and after investigator disturbance. Sample sizes are shown above bars. Different shades denote significance ($P < 0.05$).

both periods after disturbance (Wilcoxon sign rank tests; $P < 0.05$). Wingpulls were also more frequent during the first 30 min after disturbance than during the after(2) period ($Z = -2.3$, $P = 0.02$). Other pairwise comparisons were not significantly different ($P > 0.1$). The differences in the frequencies of beakpulls ($\chi^2 = 6.1$, df = 3, $P = 0.11$) and fights ($\chi^2 = 7.1$, df = 3, $P = 0.07$) among the four sampling periods approached significance. Fighting occurred infrequently in all time periods ($\bar{x}$ ± 1 SE frequency/0.5 h: before 0.2 ± 0.1, during 0.9 ± 0.2, after 0.5 ± 0.2, after[2] 0.3 ± 0.1).

There were also significant differences in the duration of wingpulls (H = 10.0, df = 2, $P < 0.01$) and beakpulls (Kruskal-Wallace ANOVA; H = 15.2, df = 2, $P < 0.01$) before, during, and after (after and after[2] pooled) disturbance (Fig. 2). Wingpulls were shorter during disturbance than before (Mann-Whitney: $Z = -3.1$, $N_1 = 36$, $N_2 = 13$, $P = 0.002$)

or after disturbance ($Z = -2.5$, $N_1 = 17$, $N_2 = 13$, $P = 0.0128$). The duration of beakpulls was also shorter during disturbance than before (Mann-Whitney *U*-test: $Z = -3.1$, $N_1 = 25$, $N_2 = 16$, $P = 0.0019$) or after ($Z = -3.5$, $N_1 = 18$, $N_2 = 16$, $P = 0.0004$). There were no differences in the duration of beakpulls ($P > 0.05$) or wingpulls ($P > 0.05$) before and after disturbance.

Chick movement and behavior.—Chick movement data and adult attacks on chicks were recorded from the onset of hatching (15 May) until all eggs from peak clutches had hatched (31 May). The first chick to stray from its natal territory was recorded on 21 May, and chick movement increased steadily thereafter until visits into the colony were terminated 31 May. Therefore, analysis of chick movement was restricted to data collected 21–31 May (N = 10 days); the number of chicks in the study plot ranged from 50 to 95.

There were significant differences in the numbers of chicks departing from their natal territories (Fig. 3A) among the four time periods (Freidman: $\chi^2 = 9.6$, df = 3, $P = 0.0219$). Pairwise comparisons revealed that significantly more chicks departed from their territories during disturbance than before (Wilcoxon sign-rank: $Z = -2.4$, $P = 0.0168$), after ($Z = -2.2$, $P = 0.0278$), and after(2) ($Z = -2.1$, $P = 0.0325$) disturbance. Other pairwise comparisons were not statistically different ($P > 0.05$). There were also significant differences in the numbers of chicks returning to their natal territories (Fig. 3B) among the four time periods (Friedman: $\chi^2 = 16.2$, df = 3, $P = 0.001$). More chicks returned after disturbance (usually within five min after the investigator returned to the blind) than before ($Z = -2.5$, $P = 0.0112$), during ($Z = -2.4$, $P = 0.0169$), and after(2) disturbance ($Z = -2.0$, $P = 0.0418$). In addition, more chicks returned during disturbance than before disturbance ($Z = -2.0$, $P = 0.0422$). Other pairwise comparisons were not statistically different ($P > 0.05$).

Although investigator disturbance increased chick movement, the proportion of chicks straying during disturbance was relatively low; range 2% (1 of 50 chicks, 21 May) to 17% (15 of 89 chicks, 29 May) per day (i.e., 30 min). Relatively few chicks (<5% per day) aged one to six days strayed from their territories during disturbance (Fig. 4). However, there was a steady increase in the percentage of chicks straying off their natal territories from age 7–13 days. In total, over the 10-day period, 53 chicks strayed from their natal territories during investigator disturbance and all but one returned within 24 h. This chick was missing and presumed dead.

Point sampling also revealed that more chicks were off their natal territories during investigator disturbance (3×2 contingency table: $\chi^2 = 13.69$, df = 2, $P < 0.005$) even though the number of stray chicks was

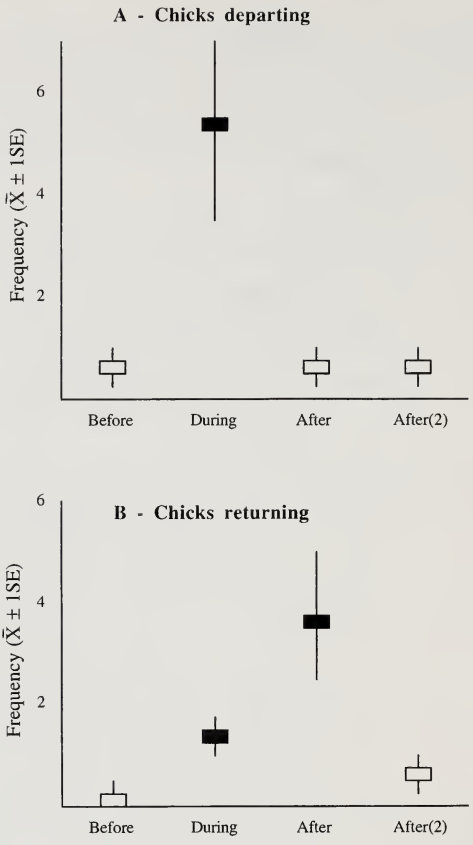

FIG. 3. The mean number (± 1 SE/0.5 h, N = 10 per sampling category) of Ring-billed Gull chicks departing from (A) and returning to (B) their natal territories before, during and two consecutive 0.5 h periods after investigator disturbance. Different shades denote significance ($P < 0.05$) except chicks returning during vs after(2) ($P > 0.1$).

low; overall, 91% of the chicks observed during disturbance were on their natal territory (Table 1). Chicks were also less active during disturbance (13%) than before (42%) and after (50%) disturbance ($\chi^2 = 110.66$, df = 2, $P < 0.01$).

Adult–chick interactions.—There were significant differences in the number of chicks attacked among the four time periods (Fig. 5: Freidman rank test; $\chi^2 = 9.2$, df = 3, $P < 0.05$). Data represent the number of individual chicks attacked (i.e., a chick attacked more than once in a sampling period was scored once). Significantly more chicks were attacked during disturbance than before (Wilcoxon sign rank test: $Z = -2.2$, $P < 0.05$) and after(2) disturbance ($Z = -2.1$, $P < 0.05$). The difference

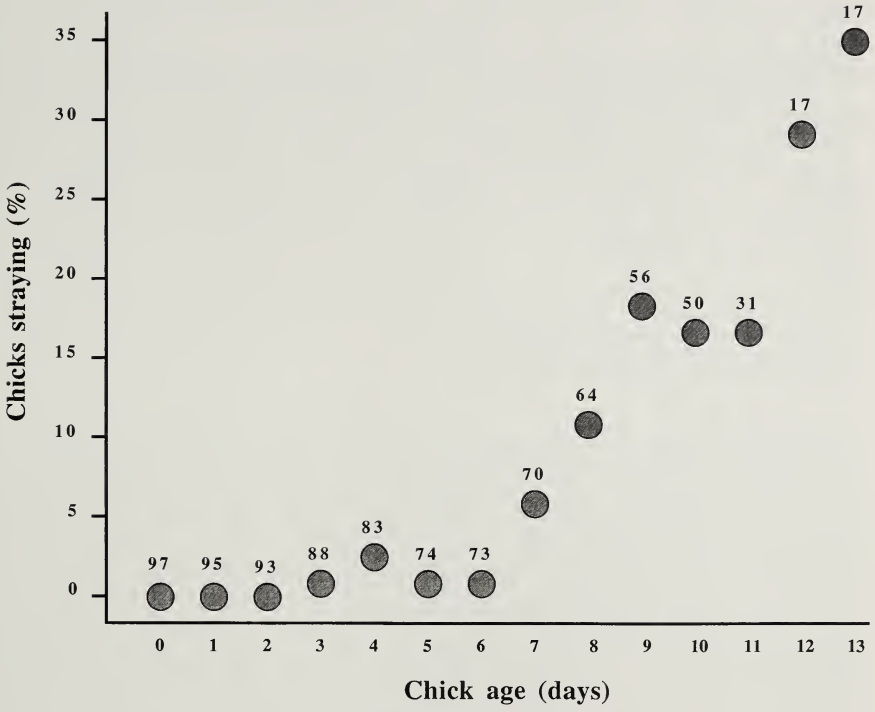

FIG. 4. The proportion of each age class of Ring-billed Gull chicks straying off their natal territories during investigator disturbance. The number above the circle represents the number of chicks in each age class.

between the number of chicks attacked during disturbance and the first 30 min after disturbance approached significance ($Z = -1.8$, $P = 0.07$). Other pairwise comparisons were not significant (before vs after $P = 0.1$, after vs after(2) $P = 0.1$, before vs after(2) $P > 0.1$). Although investigator disturbance increased the number of chicks attacks, the relative number attacked was low and none of the attacks observed during or after disturbance was fatal.

DISCUSSION

Many of our results can be compared with an earlier study by Fetterolf (1983b) that led to his claim that investigator disturbance confounded data from studies in which disturbance was not controlled. As our results vary somewhat from his, we contrast the two sets of data in the context of experimental procedures that yielded them.

As the investigator moved from nest to nest, adults scurried across

TABLE 1

THE NUMBER OF ACTIVE AND INACTIVE RING-BILLED GULL CHICKS ON OR OFF THEIR NATAL TERRITORIES BEFORE, DURING AND AFTER INVESTIGATOR DISTURBANCE

Disturbance period	Chicks on territory		Chicks off territory	
	Active[a] N (%)	Inactive[b] N (%)	Active[a] N (%)	Inactive[b] N (%)
Before	92 (41)[c]	131 (58)	3 (1)	0 (0)
During	15 (6)	203 (85)	17 (7)	3 (1)
After	115 (49)	113 (48)	3 (1)	6 (3)

[a] Active chicks were standing, wandering, begging, or being fed.
[b] Inactive chicks were hiding, crouching, or being brooded.
[c] The percent of the total is shown in parentheses.

territorial boundaries, facilitating aggression from the resident pairs towards intruding adults. Not surprisingly, we found that investigator disturbance increased the number of aggressive interactions among adults; charging and jabbing the beak at intruders increased two-fold during disturbance. Fetterolf (1983b) found that investigator disturbance increased the level of adult aggression approximately 10–15 times that observed prior to disturbance. We observed that slow movement by the investigator through the colony decreased the number of displaced adults, and localized disturbance effects into the immediate vicinity (1 or 2 m) of the investigator. Our assistant visited each nest once in a systematic fashion, usually checking several nests before moving, and returned to the blind when the nest check was complete (usually 30–60 min). This procedure

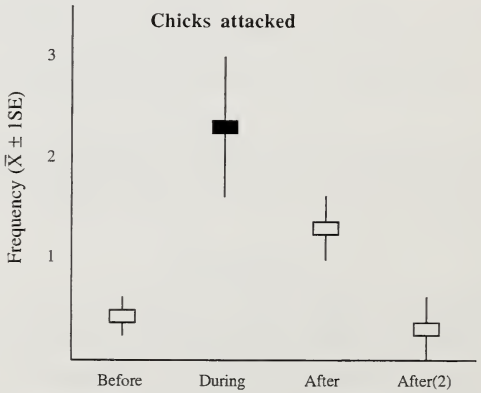

FIG. 5. The mean number (1 SE/0.5 h, N = 10 per sampling category) of Ring-billed Gull chicks attacked by adults before, during and two consecutive 0.5 h periods after investigator disturbance. Different shades denote significance ($P < 0.05$).

localized and minimized disturbance effects to the area within the study plot in which the investigator was working, usually displacing adults from their nests once per visit. In contrast, Fetterolf's assistant walked the perimeter of his 'moderately' disturbed plot spraying chicks with a weak picric acid solution from a plant mister which likely caused considerable disturbance in the adjacent, 'most' disturbed study area as well. We found that the duration of wingpulls and beakpulls decreased during investigator disturbance and that physical contests rarely escalated into a prolonged fight. This may have been because displaced gulls were not motivated to fight, behaved submissively and returned quickly to their own territories.

When an intruder enters a colony, chicks have two behavior options; they can hide or they can run. Like Fetterolf (1983b), we found that investigator disturbance increased chick movement. However, in contrast to Fetterolf, we found that relatively few chicks strayed off their natal territories during disturbance and that all but one returned after disturbance. Most chicks were inactive during disturbance and hid in the natal territory; chicks were frequently observed crouching in the same crevice as they did during non-disturbance times. The difference in the magnitude of chick displacement between our study and Fetterolf's (400–600 fold increase) may reflect differences in 1) the availability of nest cover between the two colonies, 2) the disturbance protocol, 3) nest density, and 4) the sampling method (also see Brown and Morris 1994). We consider these in turn.

First, the Mugg's Island Lake Ontario colony studied by Fetterolf was a sand bar with little vegetation or cover, whereas our colony was located on a rockpile that provided an abundance of rocky crevices in which chicks could hide. Graves et al. (1984) also noted that chicks ran more frequently when cover was sparse. Therefore, the abundance of suitable hiding places in close proximity to their natal territory may influence whether a chick runs or hides during disturbances. Second, we found that chick movement increased with age, so we stopped entering the study area once hatching was complete (31 May) and chicks were marked. This eliminated disturbance effects when chicks were older and more mobile. Although some chicks (N = 5) in the study area were 14 days old and fully mobile (Fig. 4), the procedures used in this study reduced problems associated with disturbance. Conversely, Fetterolf continued to disturb his gulls until the youngest chick was seven days old while chicks hatching earlier would have been 28–38 days old. Third, nest density has been found to increase the frequency of aggressive interactions among conspecifics (Hunt and Hunt 1976, Fetterolf 1984, Pierotti and Bellrose 1986). In 1991, nest density in our study plot (1.2 nests/m^2) was greater than that recorded in Fetterolf's plots (range: 0.5–0.7 nests/m^2) and so

cannot account for the lower levels of aggression recorded during this study.

Finally, sampling methodologies differed between the two studies. We recorded the movements of individual chicks and were able to determine whether chicks were departing from or returning to their natal territories. In contrast, Fetterolf recorded chick runs where a new run was scored if the chick paused for five or more seconds. The latter method is somewhat misleading and overestimates chick movement because five chick runs may be five different chicks running once each or one chick running five times. In our study, chicks that strayed were usually older than one week, ran less than 1 m off their territory, and crouched in nearby cover. Parsons (1982) also observed Herring Gull chicks from "open" nests hiding in nearby vegetation during nest checks. Graves et al. (1984) observed that older chicks would run, rather than hide, during disturbances. Similarly, Burger (1981) found that Herring Gull chicks that were frequently handled responded to investigators by straying farther from their nests, and ran at a younger age, than chicks not previously handled. We also noticed that picking chicks up to check leg bands and dye spots increased the likelihood that these chicks would run after being returned to the nest. Therefore, we reduced chick movement by avoiding unnecessary handling of chicks and by placing handled chicks head first into a rock crevice near the nest scrape (see Rodgers and Burger 1981).

Although the differences in chick movement between our study and Fetterolf's are of interest, the fate of mobile chicks after departure by the investigator has more important consequences for their welfare. In both studies, investigator disturbance increased the number of individual chicks attacked (this study) and the frequency of attacks on chicks (Fetterolf 1983b). In this study, chicks that remained on territory and those that strayed short distances were rarely attacked because their immediate neighbors were also displaced from their territories. However, chicks that strayed greater distances were frequently attacked, occasionally by numerous adults. In contrast to Fetterolf who reported that his activities within the colony led to human-induced chick mortality, we found that, even though our activities increased chick movement and adult aggression towards wandering chicks, none of the attacks on chicks during or after disturbance was fatal. We observed that the chicks attacked were usually older than one week and more resilient to attacks, and that they were able to return to the safety of their own territory or find cover until attacks subsided. Finally, we found that the fledging success of pairs disturbed during this study ($\bar{x} \pm 1$ SD: 1.5 ± 0.8 chicks per pair) was not different from that recorded for undisturbed pairs (1.6 ± 0.8) at this colony during 1991 (see Brown and Morris 1994).

There are many types of human disturbances in seabird colonies (Rodgers and Burger 1981) and the responses by the birds are varied (Burger 1981, Brown and Morris 1994). We have shown here that awareness of and attention to the potential impacts can reduce and even eliminate the negative consequences associated with investigator disturbance. Since many variables influence the degree to which colonial waterbirds are impacted by human disturbances including species, colony type, and location (Rodgers and Burger, 1981), we suggest that it is the ethical responsibility of every field biologist to investigate the potential consequences of experimental protocols on the individual animals and to use procedures that minimize disturbance effects.

ACKNOWLEDGMENTS

We thank Ian Kidd (International Marine Salvage) and the St. Lawrence Seaway Authority for their permission to work at the mainland and breakwall colonies, Jeffery P. Bruce, Gary P. Burness and Michael Killoran for their care and persistence in the field, and Joanna Burger and Raymond Pierotti for their helpful comments and suggestions during the review process. We also thank the Natural Sciences and Engineering Research Council of Canada, for continuous funding to RDM (research grant A6298) in support of this and other programs, and the Ontario government for financial support of KBM in the form of two Ontario Graduate Scholarships.

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Wilson Bull., 107(1), 1995, pp. 153–164

A TEST OF AN ASSUMPTION OF DELAYED PLUMAGE MATURATION HYPOTHESES USING FEMALE TREE SWALLOWS

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Abstract.—The Tree Swallow (*Tachycineta bicolor*) is one of only two North American birds in which females, and not males, have delayed plumage maturation. The hypothesis that plumage differences are the result of differences in competitive abilities among individuals is tested by comparing brown and blue Tree Swallow females in terms of foraging abilities, as determined by the growth of nestlings under their care without the help of the males, and in terms of body size and nutritional condition. Blue and brown females were not different when comparing the growth and fledging success of nestlings under their care. Blue females were larger and, even after accounting for body size differences, heavier and in better body condition than brown females. While brown plumage serves to reduce male aggression, blue plumage probably serves as a signal of dominant status in intrasexual confrontations. This signalling system is not open to cheating because of the larger size and better body condition of blue females. *Received 26 Aug. 1993, accepted 30 Jan. 1994.*

About 35 species of sexually dichromatic North American passerines have delayed plumage maturation in which males have a dull, sometimes female-like plumage during their first potential breeding season (Rohwer et al. 1980). Although these males attain sexual maturity after one year, they often fail to breed during their first potential breeding season (e.g., Rohwer et al. 1980, Procter-Gray and Holmes 1981, Studd and Robertson 1985, Lyon and Montgomerie 1986). Delayed plumage maturation of females and not males has been reported only for Hooded Warblers (*Wilsonia citrina*) (Morton 1989) and Tree Swallows (*Tachycineta bicolor*) (Hussell 1983). Tree Swallows also differ from other North American passerines that show delayed plumage maturation in that most adults over two years old are sexually monochromatic. Most females in their first potential breeding season are dull brown, but a few are iridescent blue-green, like most older females and all males (Hussell 1983). Although these brown females are sexually mature (DeSteven 1978), few manage to become breeders (Kuerzi 1941, Stutchbury and Robertson 1985).

Several hypotheses have been proposed to explain the adaptive significance of delayed plumage maturation: (1) cryptic (Selander 1965, 1972; Procter-Gray and Holmes 1981), (2) female-mimicry (Rohwer et al. 1980), (3) breeding threshhold (Studd and Robertson 1985) and (4) status signalling (Lyon and Montgomerie 1986) hypotheses. One assumption

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common to these is that differences in plumage are the result of variation in the ability of individuals to obtain breeding opportunities. Using female Tree Swallows, we tested this assumption by examining two factors that could affect both how early females can arrive to the breeding grounds to obtain territories, and their ability to defend these territories thereafter. Blue and brown females are compared in terms of size, nutritional condition, and their ability to raise offspring without male help. We assumed that differences in their ability to raise offspring would be a reflection of the females' foraging abilities. Foraging ability is important when food availability is low, and would affect how early in the spring females can arrive to the breeding grounds.

METHODS

We conducted the study in 1990 at a Tree Swallow colony surrounding two sewage lagoons near Tweed, Ontario, Canada (44°29′N, 77°26′W). This colony has been occupied since 1983. Fifty-three nest boxes (14 × 14 × 33 cm, 3.85 cm diameter entry hole) were available, plus another twelve smaller boxes that were not used in any experiments, although some nestlings from these boxes were used in the first experiment. Each large box was fitted with a bird trap and was approximately 1.5 m above ground, attached to metal or wooden poles. To prevent predation, the poles were fitted with conical metal shields or maintained with copious amounts of grease for the duration of the breeding season. The boxes were placed around the lagoons at approximately 20 m intervals, with the entrance holes all facing south.

The first experiment tested whether blue females were better than brown females at raising offspring. Because the abundance of flying insects changes during the breeding season (Quinney et al. 1986), the procedure involved locating pairs of boxes, one of each pair being occupied by a brown and the other by a blue female, whose eggs had hatched on the same day. The sample size was limited by the availability of such pairs. Females whose plumage was intermediate between brown and blue were not used.

For each such pair, on the morning of day 4 (hatch = day one), nestlings of these two boxes plus all other nestlings in the colony at the same stage of development were weighed and individually marked. In the afternoon of day 4, the two experimental boxes were randomly assigned six young each taken from this pool. One pair of nests received only five young each because only 10 nestlings were available. Assigned young were obtained from the subset of those nestlings banded in the morning that excluded both extremely large and small chicks. Therefore, each female ended up raising relatively uniform-sized young, some of which may have been originally her own. This removed any potential correlations between the quality of parents and their young. The following morning the young were visually checked to confirm that the parents had accepted all young as their own. To remove any confounding effect males might have, by compensatory feeding for example, they were removed on the afternoon of day 5.

Nestlings were checked daily until they fledged or died, and on days 10 and 15 the mass, wing chord, and ninth primary feather length of each young were measured. Differences in the survival and growth of the young at days 10 and 15 and the fledging success were assessed using a Wilcoxon Matched-pairs Signed-ranks test.

Starting in the last week of April 1990, females were sequentially removed from nest boxes. These birds were not the same used in the previous experiment, and again, females

of intermediate plumage were not used. Dissections were carried out to confirm the birds' sex. The birds were then weighed, bagged, and frozen. Birds were collected only during the mornings. All females collected were measured and analyzed to determine if blue females are larger and/or in better nutritional condition than brown females. For each carcass the following structural measurements were recorded: wing chord (mm), ninth primary (mm), left tarsus (0.01 mm), keel length (0.01 mm), body length (mm), and middle rectrix (mm). The birds were then weighed to the nearest 0.01 g, and reweighed after being plucked and after the reproductive organs and contents of the intestinal tract had been removed. The carcass and reproductive organs were dried to a constant mass, extracted with petroleum ether in a Soxhlet apparatus, and then burned overnight in a muffle furnace to determine the amount of ash. The ash value was subtracted from the residue of the ether extraction to determine the ash free lean dry weight, which was used as an index of protein for each bird (Dobush et al. 1985).

Differences in size were analyzed with a MANOVA using all six morphological measurements. To account for body size when comparing body composition and nutrient reserves, a principal components analysis (PCA) was carried out on the correlation matrix of the six morphological measurements, and then each body composition variable was regressed against the resulting first principal component (PC1), which was taken to be an indicator of size (Rising and Somers 1989). The residuals of all significant regressions were added to the respective mean to obtain body condition values adjusted for size (Steel and Torrie 1980). These adjusted values were used to test the effects of plumage color on body composition, using type III sums of squares ANCOVAs with plumage color, date of capture, and color-date of capture interaction effects. Interaction effects were included to test if the effect of color differed depending on the date of capture, and were removed from the model if not significant.

RESULTS

Fourteen clutches were available for this experiment. Two of these, both belonging to blue females, were lost to predators. To obtain balanced analyses, data for the corresponding brown female boxes were removed from all comparisons between the two treatments. Young in any one box were a subset of all those form the colony at the same developmental stage, some of which might have been originally from that same box. It is possible that females preferentially fed their own young; however, there were no significant differences in survivorship between the chicks that remained in the box where they hatched and those that were moved (day 10 $\chi^2 = 0.032$, 1 df, $P > 0.90$; day 15 $\chi^2 = 0.371$, 1 df, $P > 0.50$; fledging $\chi^2 = 0.513$, 1 df, $P > 0.25$).

No differences between brown and blue nests were found in the percent of nestlings surviving to day 10 (Wilcoxon Matched-pairs Signed-rank test, $Z = 1.000$, $P = 0.3173$) or day 15 ($Z = 1.000$, $P = 0.3173$), nor in the number ($Z = 1.4832$, $P = 0.1380$) or percent ($Z = 1.4832$, $P = 0.1380$) of young fledged. However, in four out of five pairs blue females fledged more young than brown females (Table 1).

To account for the initial variation in size when comparing the growth of nestlings, masses, wing chord and ninth primary feather lengths of the

TABLE 1
SURVIVAL OF TREE SWALLOW NESTLINGS RAISED BY BROWN (BR) OR BLUE (BL) FEMALES

Hatch date (June)	Number per nest	Number alive							
		Day 10		Day 15		Fledged		Percent fledged	
		BR	BL	BR	BL	BR	BL	BR	BL
5	6	6	6	6	6	4	6	0.666	1.000
6	6	6	6	6	6	4	5	0.666	0.833
7	6	6	5	6	2	0	2	0.000	0.333
7	5	5	5	5	5	4	5	0.800	1.000
13	6	6	6	3	3	2	1	0.333	0.166

nestlings at days 10 and 15 were regressed separately against masses at day 4. Values adjusted for initial size were obtained using the residuals of these regressions, from which a mean for each nest was calculated. These means were used in Wilcoxon Matched-pairs Signed-ranks tests. No differences in wing chord lengths were found at day 10 ($Z = 1.21136$, $P = 0.2249$) nor day 15 ($Z = 0.4045$, $P = 0.6858$). Comparisons using the ninth primary feather lengths did not produce significant differences either ($P > 0.30$), and showed the same pattern.

Only for mass at day 10 (Fig. 1) was the difference between the two treatments significant ($Z = 2.0226$, $P = 0.0431$). On day 10, nestlings being raised by brown females were heavier than those being raised by blue females. This is the exact opposite of the expected result. These differences, however, were not evident by day 15 ($Z = 0.4045$, $P = 6858$) (Fig. 1).

Blue females were bigger than brown ones when taking all variables into account (MANOVA $P = 0.03$). Except for keel length, the means of blue females were higher than those of brown females and, using univariate tests, only the length of the 9th primary feather differed significantly (Table 2).

To account for body size when comparing body composition and nutrient reserves, a principal components analysis (PCA) was carried out on the correlation matrices of the six morphological measurements. The first principal component (PC1) was positively correlated with all morphological measurements and accounted for 44.8% of the total variance. Except for gonad weight, all regressions of body composition variables against PC1 were significant (Table 3). Values adjusted for size (PC1) were used on all subsequent analyses.

When comparing these size-adjusted values, there were significant color·date interaction effects for carcass weight (Table 4). This indicates that

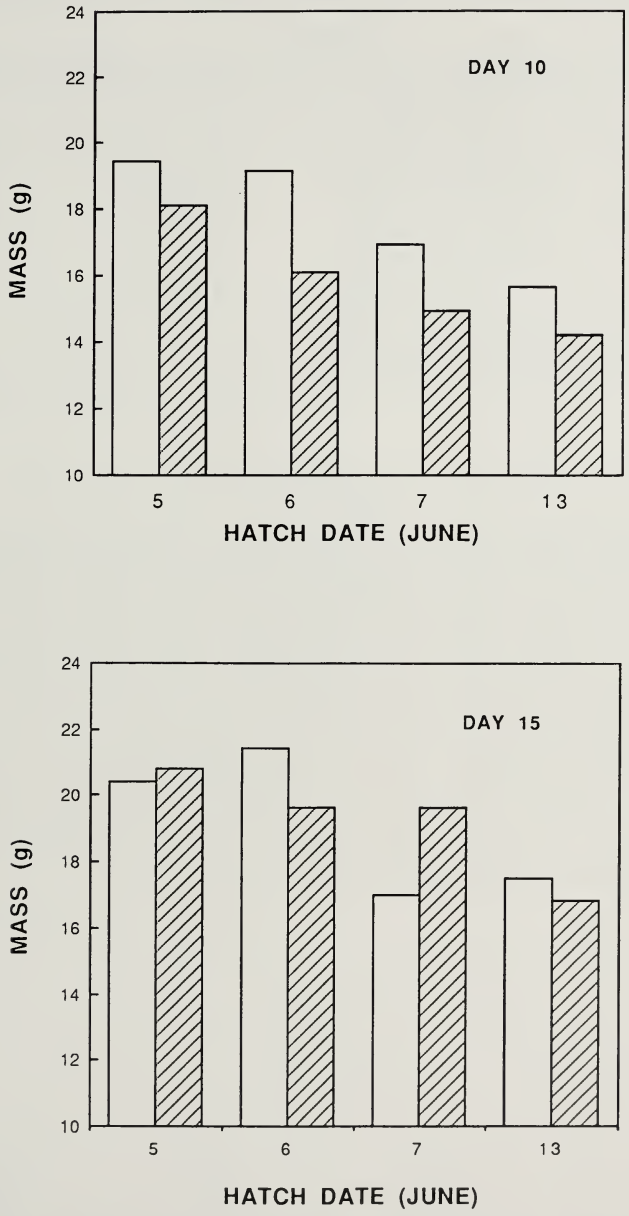

FIG. 1. Mass of Tree Swallow nestlings at 10 and 15 days after hatch. Values were adjusted for mass at day 4. Open bars = brown females, Lined bars = blue females.

TABLE 2

SIZE OF BROWN AND BLUE FEMALE TREE SWALLOWS[a]

Variable	Brown females	Blue females	*P*
Wing chord	115.9 (0.526)	116.8 (0.436)	0.205
Ninth primary	89.75 (0.445)	91.50 (0.469)	0.009
Keel*	20.64 (0.113)	20.39 (0.100)	0.102
Tarsus	12.16 (0.077)	12.24 (0.079)	0.686
Body	149.64 (0.559)	150.75 (0.442)	0.147
Rectrix	46.64 (0.360)	46.97 (0.309)	0.523

* N = 57 because of one brown female with a broken keel.

[a] A MANOVA using all morphological variables yielded a *P* value of 0.030. Shown are the mean lengths (mm), SE and *P* values from univariate *F*-tests (N = 58; 26 brown, 32 blue).

the effect of plumage color was dependent on the capture date. This was because the mass of blue females did not change during the removal period (linear regression, $P = 0.3248$), but there was a significant drop in mass with time for brown females ($P = 0.038$) (Fig. 2). Similarly, the color·date of capture interaction effects were also significant for both dry mass and fat content (Table 4), but in both cases there were significant ($P < 0.05$) seasonal declines for both brown and blue females.

For ash and protein measures, there were no significant color·date interaction effects. Blue female values were significantly greater than those of brown females (Table 4, Figs. 3, 4). For protein there was a significant seasonal decline ($P < 0.001$, Fig. 3), whereas ash content was significantly higher ($P = 0.016$) in those birds captured later in the season (Fig. 4). There were no differences in gonad mass (Table 4).

TABLE 3

RELATION OF BODY COMPOSITION AND NUTRIENT RESERVES TO SIZE (PC1) IN FEMALE TREE SWALLOWS

Variable	Slope	*P*	r^2
Gonad mass	0.001	0.939	0.00011
Carcass mass*	0.655	<0.001	0.29122
Dry mass	0.338	0.007	0.19260
Fat	0.165	0.035	0.07968
Ash	0.022	0.015	0.10518
Protein	0.155	<0.001	0.28263

* Feathers, gonads and contents of the alimentary tract excluded; N = 58.

TABLE 4

THE EFFECT OF PLUMAGE COLOR AND DATE OF CAPTURE ON THE BODY COMPOSITION AND NUTRIENT RESERVES OF FEMALE TREE SWALLOWS VALUES ADJUSTED FOR BODY SIZE WERE USED IN ALL CASES[a]

Variable	Plumage color	Date of capture	Color-date interaction	r^2
Carcass mass*	0.588	0.068	0.055	0.283
Dry mass	0.032	<0.001	0.006	0.493
Fat	0.013	<0.001	0.019	0.438
Ash	0.003	0.016	—	0.197
Protein	0.050	<0.001	—	0.302
Gonad mass	0.132	0.002	—	0.177

* Feathers, gonads and contents of the alimentary tract excluded.
[a] The interaction term was removed from the model if not significant (N = 58; 26 brown, 32 blue).

DISCUSSION

Differences in foraging ability could be one way in which blue females might have a competitive advantage over brown ones. Brown females are known to have lower egg mass, clutch size, brood size, and fledging

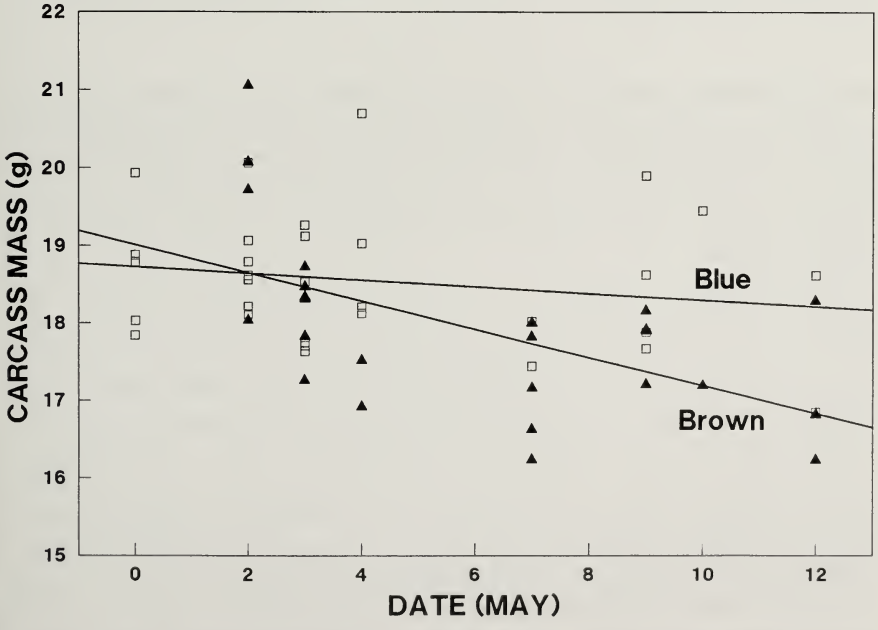

FIG. 2. Mass of Tree Swallow females with respect to plumage color and date of capture. Brown = ▲, blue = □.

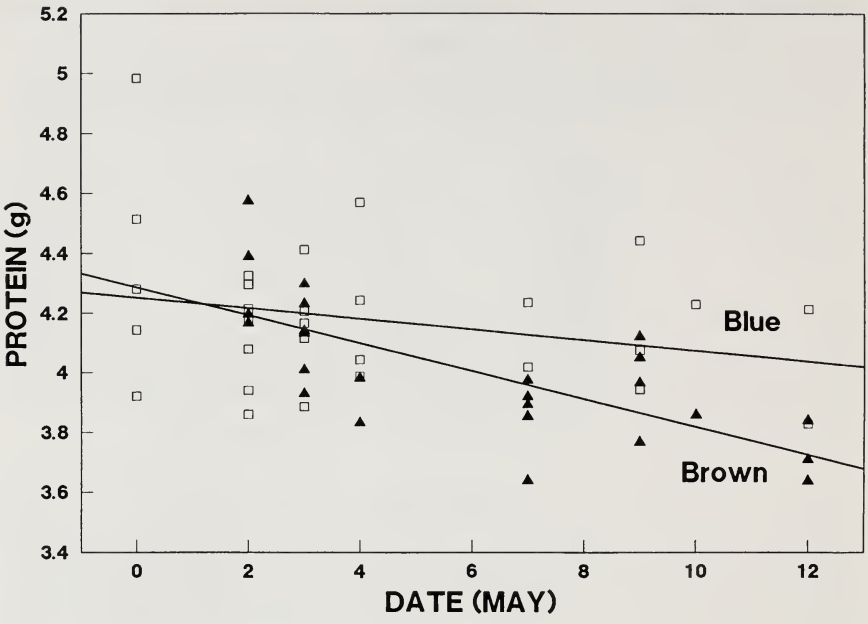

FIG. 3. Protein of Tree Swallow females with respect to plumage color and date of capture. Brown = ▲, blue = □.

success (DeSteven 1978), but DeSteven (1980) concluded that these were not caused by differences in foraging efficiency because both brown and blue females could easily rear additional young. Her study (DeSteven 1980), however, failed to account for the possibility that males could have compensated for any foraging ability differences that might have existed among females.

In this study the males were removed first, and only then was the growth of nestlings compared. There were no replacement males in any of the experimental nests. Because feather growth of nestling Tree Swallows continues after mass gain has been completed (Zach and Mayoh 1982), it was expected that mass differences would more likely be detected at day 10, and feather growth differences at day 15. Consistent with this, the clearest result across the entire hatch date range was obtained for mass at day 10, but contrary to the predictions, nestlings raised by brown females were heavier than those being raised by blue females. These differences, however, had disappeared by day 15. These results show that brown females who manage to breed are able to deliver food to their young as well as, and sometimes even better than, blue females.

If we accept the notion that, if not due to senility, foraging ability

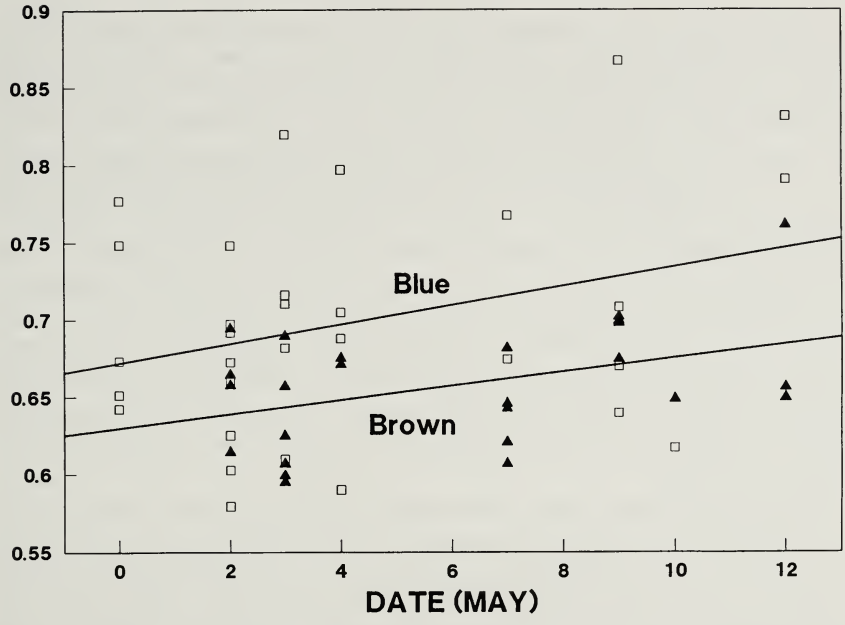

FIG. 4. Ash content of Tree Swallow females with respect to plumage color and date of capture. Brown = ▲, blue = □.

cannot possibly decrease with age, why did some young raised by brown females grow faster? One possible explanation is that we did not measure foraging ability per se but rather differences in levels of maternal care. There is great variation in feeding rates in swallows as responses to various weather conditions, artificially manipulated brood sizes, and temporary removals of mates (Kuerzi 1941, Leffelaar and Robertson 1986). It is possible that blue females maintain an optimum feeding rate for the conditions in which they find themselves, while brown females simply feed their young at the maximum rate they can. The greater effort of brown females seems to be futile because by day 15 any differences that were observed at day 10 no longer occurred. More importantly, there were no differences in the survival to days 10 and 15, nor in the fledging success.

Another way in which brown females might be at a competitive disadvantage could be in terms of size and nutritional condition. For this part of the study females were collected prior to engaging in reproduction; this eliminated any effects different patterns of maternal care might have on their nutritional condition.

When comparing size, only the length of the primary feather was sig-

nificantly larger in blue females, but the means of all the other variables, except keel length, were also higher for blue females (Table 3). With respect to nutrient reserves, later in the season blue females were heavier and fatter than brown females, but there were no differences earlier in the season. This could be because brown females captured earlier in the season were replacements of previously removed birds, and they are being compared to blue females that had arrived earlier and taken on the costs of nest defense for up to several days, having thus exhausted their reserves. Because the birds were captured as soon as nest building was initiated they were still far from egg laying and no differences in gonad masses were expected. However, differences in protein and ash content indicate that blue females had more resources available to allocate to egg production than brown females. Therefore, blue females could have engaged in reproduction faster than brown females, as soon as the conditions became favorable.

These comparisons were made after correcting for body size, so it is not merely that larger birds are heavier and in better nutritional status. These results indicate that, for any given size, blue females are in better condition than brown females. This could have many implications for their reproductive tactics, perhaps explaining the lower clutch size of brown females (Stutchbury and Robertson 1988). In terms of intrasexual competition for breeding opportunities, a larger and heavier body could affect both the thermoregulation and the fighting ability of females.

Larger birds carry more energy relative to their size and therefore can better tolerate periods of food shortage (Blem 1990). In the study area, night temperatures during April can be low enough for frost to build. These low temperatures, often combined with rain, not only decrease the number and activity of flying insects, but also put swallows under severe thermal stress. Swallows may reduce the demands of thermoregulation by roosting (Stutchbury and Robertson 1990), but continued or extremely low temperatures will unavoidably result in death (Weatherhead et al. 1985, Lombardo 1986a). The larger body size and better condition of blue females should better enable them to withstand these conditions. This also explains why blue females arrive at the breeding grounds earlier than brown females (Kuerzi 1941).

One important advantage of an early arrival is the increased likelihood of obtaining one of the limited number of nest sites. Tree Swallows often engage in violent fights for the possession of nest boxes, which may result in evictions of resident birds (Kuerzi 1941, Leffelaar and Robertson 1985) and sometimes even in deaths (Kuerzi 1941, Lombardo 1986b). There is some anecdotal evidence (Leffelaar and Robertson 1985) showing that, while ignoring empty nest boxes, females fight among themselves for nest

boxes already occupied by males; this suggests that males obtain the nesting cavities first and that females then choose among them. Therefore females may not be limited by the availability of nest boxes per se, but rather by the availability of nest sites with males. Blue females, being in better condition and slightly bigger than brown females, would be at an advantage in any physical confrontations for such nest sites.

Resident male Tree Swallows do not show much hostility towards brown conspecifics, but resident females are equally aggressive towards all intruders (Stutchbury and Robertson 1987). This provides a proximate function for the brown plumage, but it fails to explain why females moult into a blue plumage before their second potential breeding season. Given that brown plumage decreases the aggression from conspecific males, Stutchbury and Robertson's findings have changed the question from: "Why should a female be brown in her first year?", to: "Why should a female be blue in her second year?". There must be some advantage(s) to being blue that outweigh(s) the costs of increased male aggression. While brown plumage serves to decrease aggression from males (Stutchbury and Robertson 1987), blue plumage may function as a signal of dominant status towards females in intrasexual confrontations (Lyon and Montgomerie 1986). For such a signalling system to be stable and not open to cheating, differences in plumage would have to be associated with competitive differences (Rohwer 1982). The fact that blue females were found to be slightly larger and in better body condition than brown females supports this idea.

By definition, color and age are correlated in species with delayed plumage maturation so these results do not negate age as a factor; they simply provide a possible explanation for what it is about age that generally causes Tree Swallow females to be brown in their first potential breeding season and blue thereafter. It would be interesting to determine if blue females are also bigger and in better nutritional status than brown ones among yearlings.

ACKNOWLEDGMENTS

We thank D. Ankney and T. Laverty, for their constant discussions throughout the study, T. Quinney for offering the use of his colony, D. Hussell for his comments during the initial stages of the study, J. Amery and S. Hatch for helping with the carcass analyses, and B. Montgomerie, B. Stutchbury and an anonymous reviewer for their comments on a previous draft. The Collip 112 crowd (K. Dufour, S. Lougheed, R. Moses, and Mr. Yezerinac) contributed greatly to the initial analyses and writing. This study was financially supported by NSERC, the Canadian Wildlife Service, and the Sigma Xi Society.

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Wilson Bull., 107(1), 1995, pp. 165–169

SHORT COMMUNICATIONS

Capsaicin detection in trained European Starlings: the importance of olfaction and trigeminal chemoreception.—Although the morphological organization of the peripheral trigeminal system in birds is not very different from that found in mammals (Dubbledam and Veenman 1978), broad functional differences exist (Kare and Mason 1986; Mason et al. 1989, 1991b; Norman et al. 1992). For example, birds rarely avoid mammalian irritants, even though the avian trigeminal system is responsive to chemical stimuli (Walker et al. 1979, Mason and Silver 1983, Mason et al. 1989). Rock Doves (*Columba livia*), Red-winged Blackbirds (*Agelaius phoeniceus*), European Starlings (*Sturnus vulgaris*), and Gray Partridges (*Perdix perdix*) are indifferent to ammonia (Soudek 1929, Mason and Otis 1990). Parrots (*Amazona* spp., Mason and Reidinger 1983a), Rock Doves (Szolcsanyi et al. 1986), Red-winged Blackbirds (Mason and Maruniak 1983), European Starlings (Mason et al. 1991a), House Finches (*Carpodacus mexicanus,* Norman et al. 1992), and Cedar Waxwings (*Bombycilla cedrorum,* Norman et al. 1992) are indifferent to ≥1000 ppm capsaicin, the pungent principle in *Capsicum* peppers. Likewise, Red-winged Blackbirds and European Starlings are indifferent to 1000 ppm gingerol and zingerone, the irritants present in ginger (*Zingiber officinale*), as well as to 1000 ppm piperine, the active ingredient in black pepper (*Piper nigrum*) (Mason and Otis 1990). Mammals typically avoid much lower concentrations of these substances: 100 ppm capsaicin is typically avoided by rodents (Mason, pers. obs.).

The indifference that birds exhibit towards at least some mammalian irritants may reflect both insensitivity and a relatively high tolerance for these substances independent of sensation. For example, a recent series of experiments (Mason and Clark 1994) showed that starlings can detect 1.0% [mass/mass (m/m)] capsaicin in flavor avoidance learning experiments. Such learning does not occur when 0.1% (m/m) capsaicin is used as the conditional stimulus, suggesting that this lower concentration is not perceived. Both capsaicin concentrations are strongly aversive to mammals (e.g., Silver et al. 1985).

Because birds do not appear to respond to capsaicin as an irritant, the possibility exists that detection of this substance is mediated by a sensory system other than the trigeminal system. The present experiments were designed to investigate this issue. In Experiment 1, sham-operated European Starlings and starlings with bilateral olfactory nerve cuts were presented with 1.0% (m/m) capsaicin in a conditioned flavor avoidance paradigm. In Experiment 2, sham-operated starlings and birds with bilateral olfactory and trigeminal nerve cuts were similarly trained.

Methods.—Starlings were decoy-trapped in Sandusky, Ohio, and shipped by air to the Monell Chemical Senses Center. Upon arrival, the birds were individually-caged (dimensions: 61 × 36 × 41 cm) under a 13:11 h light : dark cycle (lights on 07:00–20:00 h). Prior to testing, feed (Purina Flight Bird Conditioner, Purina Mills, St. Louis, Missouri) and tapwater were provided ad libitum.

Capsaicin (CAS# 404-86-4), ethyl ether (CAS# 60-29-7), and lithium chloride (CAS# 7447-41-8) were purchased from Sigma Chemical Company (St. Louis, Mo.). For preparation of feed samples, capsaicin was dissolved in ethyl ether and then mixed with Flight Bird Conditioner to produce a concentration of 1.0% (m/m). Control feed samples were prepared by mixing ethyl ether with plain feed. All samples were placed under a ventilation hood for 48 h to evaporate the ether (Jakubas et al. 1992) and then stored at −17°C in closed containers until 30 minutes prior to use.

In the first experiment twenty-two naive starlings were assigned randomly to three groups.

The birds in group BONC (N = 8) were given bilateral olfactory nerve cuts (Mason and Silver 1983, Clark and Mason 1987, Mason et al. 1989). Briefly, birds were anesthetized by intraperitoneal injection of sodium pentobarbital (65 mg/kg body mass) and then placed in a specially designed head holder. The two olfactory nerves underlying the bony orbital walls were exposed, lifted slightly, and 1-mm sections were removed from each. The cut nerve ends were folded back to hinder regeneration, the cavity was packed with gelfoam, and the skin closed with cyanoacrylate glue. The birds in group SHAM (N = 8) were treated identically to those in group BONC, except that their olfactory nerves were not cut. The birds in group CONT (N = 6) were not subjected to surgery.

After five days of recovery from the surgical procedure, all birds were given two-cup pretreatment trials on each of four consecutive days. On each day, all birds were presented with two food cups at 08:00 h. Both cups contained 20 g of ether-treated control feed. After two hours, the feed remaining in each cup was weighed. Between 10:00 and 17:00 h EST, all birds were provided with free access to untreated feed and tapwater. Overnight (17:00–08:00 h), birds were food deprived. The food deprivation regime remained in effect throughout the remainder of the experiment.

On the day of conditioning (day 5), all birds were given a cup containing 20 g of treated feed. After two hours, the feed remaining in the cup was weighed, and the birds in groups BONC and SHAM were gavaged with lithium chloride (2 mg/kg body mass; Mason and Reidinger 1983b, Mason and Silver 1983). The birds in group CONT were gavaged with tapwater (2 mg/kg body mass).

A four-day test period immediately followed the day of conditioning. On each of these days, all birds were given two-cup tests between 08:00 and 10:00 h. One cup contained 20 g of control feed while the other contained 20 g of treated feed. As before, the weight of feed remaining in each cup was recorded at the end of the test, and the birds were provided with free access to untreated feed and tapwater until 17:00 h.

For data analysis, pretreatment period preference ratios were calculated by dividing consumption from the left (or right) cup by overall consumption from both cups during the pretreatment period. Test period preference ratios were calculated by dividing consumption of capsaicin-adulterated feed by overall consumption from both cups.

A three-factor analysis of variance (ANOVA) was used to evaluate the results. The independent factor in this analysis was groups (3 levels), while the repeated factors were periods (2 levels) and days (4 levels). Tukey tests (Winer 1971) were used to isolate significant differences among means ($P < 0.05$).

In the second experiment the 16 sham and BONC birds again served as subjects. The birds in group SHAM were treated as previously described. Likewise, the birds in group BONC were given bilateral trigeminal nerve cuts using procedures similar to those described in experiment 1. Briefly, each bird was anesthetized and placed in the head holder. The ophthalmic branches of the trigeminal nerve were exposed by removing the gelfoam from the cavity left by the previous surgery. The nerves were then cut, and the ends were folded back to hinder regeneration. The surgical cavity was again packed with gelfoam, and the skin was closed with cyanoacrylate glue.

After five days of recovery from the surgical procedure, all birds were given two-cup pretreatment, conditioning, and test trials identical to those described in experiment 1. At the conclusion of the experiment, preference ratios were calculated, and evaluated in a three-factor ANOVA. The independent factor in this analysis was groups (2 levels), while the repeated factors were periods (2 levels) and days (4 levels). Tukey tests were used to isolate significant differences among means ($P < 0.05$).

Results.—In experiment 1, there was a significant group × period interaction ($F = 7.1$; 2,19 df; $P < 0.01$). Post-hoc tests revealed the following pattern of effects. First, the mean

FIG. 1. Mean preference ratios exhibited by starlings given bilateral olfactory nerve cuts (BONC group) or sham surgeries (SHAM group) followed by flavor avoidance conditioining with 1.0% (m/m) capsaicin adulterated food. Control group (CONT) birds were not subjected to surgery or conditioning. Capped vertical bars represent standard errors of the means.

CONT pretreatment preference ratio did not differ from the mean CONT test preference ratio. However, both the SHAM and the BONC mean pretreatment preference ratios were significantly larger than the test preference ratios for these groups (Fig. 1).

In experiment 2, there was a significant interaction between groups and periods (F = 8.51; 1,11 df; $P < 0.01$). Post-hoc tests showed that BONC pretreatment preference ratios were significantly smaller than SHAM test period preference ratios. BONC preference ratios did not change significantly between periods (Fig. 2).

Discussion.—CONT starlings failed to avoid 1.0% (m/m) capsaicin in the absence of training. This lack of response is consistent with other reports (e.g., Mason et al. 1991a, b; Norman et al. 1992; Szolcsanyi et al. 1986), and suggests that starlings are relatively less sensitive than mammals to this chemical (e.g., Silver et al. 1985). Nevertheless, starlings can be trained to avoid 1.0% (m/m) capsaicin, providing strong evidence that this species detects capsaicin as a stimulus. The qualitative nature of this stimulus remains obscure, although the present experiments provide clues as to the sensory system mediating the behavioral response.

Olfaction appears to be unimportant. Although capsaicin has a vanillin odor to humans, bilateral olfactory nerve cuts had no measurable effect on acquisition of conditioned avoidance towards adulterated foods. In addition, the experiments were conducted during November, a time of year during which starling olfactory detection and discrimination are poor (Clark and Smeraski 1990).

Contrary to expectations, an intact trigeminal nerve was important for response acquisition. This demonstrates that starlings can detect capsaicin via trigeminal chemoreception just as mammals do (Silver et al. 1985). The surprising difference between the taxa is that the mammalian trigeminal system appears to encode capsaicin as a chemically painful stimulus, while the avian trigeminal system does not. Although the present data do not address

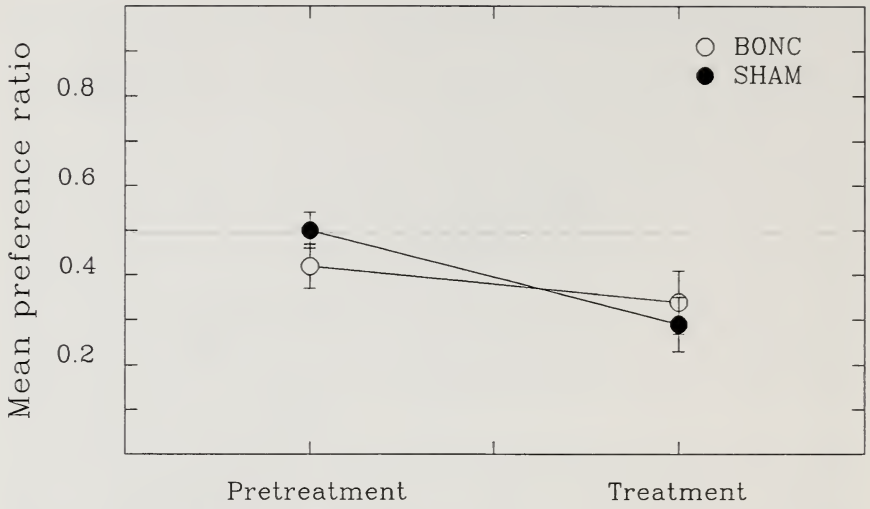

FIG. 2. Mean preference ratios exhibited by starlings given bilateral olfactory and trigeminal nerve cuts (BONC group) or sham surgeries (SHAM group) followed by flavor avoidance conditioning with 1.0% (m/m) capsaicin adulterated food. Capped vertical bars represent standard errors of the means.

the issue, we speculate that avian capsaicin detection could be mediated by thermal receptors rather than by chemoreceptors. This speculation is based on evidence that some portion of the mammalian response to capsaicin is mediated by thermoreceptors (Foster and Ramage 1981). Regardless, the results of the present investigations provide further confirmation that the chemosensory world of birds and in particular, the perception of mammalian chemical irritants, is fundamentally different from the chemosensory world of mammals.

Acknowledgments.—We thank G. Epple, E. P. Hill, and P. Moore for their comments on earlier manuscript drafts. S. L. Lewis provided able technical assistance.

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Wilson Bull., 107(1), 1995, pp. 169–174

Depredation of artificial Ovenbird nests in a forest patch.—One of the most likely causes of the decline of Neotropical migrants is the loss of suitable breeding habitat. Forest fragmentation reduces the quantity of habitat and the quality of the remaining habitat for avian reproductive success. Lower reproductive success sometimes can be caused by increased rates of nest predation, and nest predation on artificial nests may be more intense in habitat fragments than in larger, more continuous tracts of similar habitat (Wilcove 1985, Yahner and Scott 1988, Langen et al. 1991).

The Ovenbird (*Seiurus aurocapillus*) is one of several Neotropical migrant landbirds that are associated with the forest interior (Whitcomb et al. 1981, Freemark and Merriam 1986). The species appears to be declining rapidly (Ambuel and Temple 1982, Robbins et al. 1989), but we know of only one study (Hann 1937) that reported predation rates for a large number of Ovenbird nests. Consequently, our objectives were to (1) compare survival rates between artificial domed nests (mimicking that used by the Ovenbird) and artificial open-cup ground nests (typical of many Neotropical migrant species), (2) determine if artificial nests located closer to the forest/field edge exhibit lower survival rates than those located in the forest interior, and (3) compare survival rates, during a five-day cycle, throughout the breeding season.

Study area and methods.—This study was conducted in a 70-ha forest patch adjacent to the east shore of Lake Shelbyville in Shelby County, Illinois (39°N, 88°W) during spring and summer of 1991. This is the largest forest patch bordering the lake and often is referred to as the "Boot" (Robinson 1992). The Boot was selectively logged as recently as 30 years ago, and the remaining stand consists of predominantly young (<30 cm DBH) *Quercus, Aceraceae, Juglandaceae* trees. Numerous steep ravines transect the forest and become more abrupt near the lake. The Boot is surrounded by agricultural fields (soybean and corn) and Lake Shelbyville. Land acquisition for the construction of Lake Shelbyville began in 1960 by the U.S. Army Corps of Engineers, and the lake was completed in 1970. The surrounding floodplain has been left undisturbed and allowed to undergo succession since 1960. The vegetational habitat in this area is extremely heterogeneous and currently is being managed to maintain this heterogeneity (see Robinson 1992 for more details).

Possible nest predators that were identified in the Boot include the American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), eastern chipmunk (*Tamias striatus*), raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginianus*), and various snakes (Linder, pers. observ.). Additional nest predators that were probably present and have been identified in habitat similar to the Boot include red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), striped skunk (*Mephitis mephitis*), domestic cat (*Felis silvestris*), and the domestic dog (*Canis familiaris*). Population densities of potential predators were not known.

We constructed artificial open-cup nests using plastic cups (90 mm in diameter and 45 mm in depth) painted with flat black paint. Nesting material consisted of dry grasses placed in each cup. Infertile Northern Bobwhite (*Colinus virginianus*) eggs, acquired from a local game farm, were used. Artificial open-cup nests were placed in depressions in the leaf litter so that virtually no plastic was visible. We also constructed artificial domed nests, which were similar to the open-cup nests, but with a leaf litter dome to mimic the nest of the Ovenbird. Domes were built by placing leaf litter on arched twigs/branches that spanned the breadth of the nest. Open-cup nests were located near shrubs, logs, or trees, whereas domed nests were located in open areas. Seven nests of each type were placed 20, 200, and 400 m, respectively, from the forest/agricultural field edge; nests of similar type were >50 m apart, and all nests were >25 m from one another. Nests 400 m from this edge were 100–200 m from the shore of Lake Shelbyville. Small and Hunter (1988) did not find large bodies of water to act as an edge for predators associated with ground nesting birds, therefore, we refer to the area 400 m from the forest/agricultural edge as interior rather than another edge.

A single egg was added daily to each artificial nest to create the appearance of an active nest in an attempt to elicit brood parasitism (Lowther 1979, Thompson and Gottfried 1981). Four trials were conducted between 16 June and 20 July 1991. A single trial consisted of depositing an egg (between 10:00 and 12:00 CST each morning) in each nest for four consecutive days. Nest fate was recorded at each visit; a nest was considered depredated if eggs were broken or missing (Yahner and Scott 1988). Egg fragments, if present, were

TABLE 1
RESULTS OF AN ANOVA ON PREDATION OF ARTIFICIAL GROUND NESTS[a]

	df	*F*	*P*
Survival egg-days			
Nest type (N)	1	12.17	0.0374
Distance (D)	2	5.89	0.0282
Time (T)	3	7.78	0.0001
N × D	2	0.77	0.5043
N × T	3	0.95	0.4170
D × T	6	0.86	0.5268
N × D × T	6	0.53	0.7867
Predator-free days			
Nest type (N)	1	10.13	0.0372
Distance (D)	2	12.84	0.0297
Time (T)	3	6.68	0.0002
N × D	2	0.47	0.6260
N × T	3	0.79	0.5020
D × T	6	0.71	0.5273
N × D × T	6	0.66	0.6831

[a] Three effects were examined; nest type (N), distance from field (D), and time of trial (T). Nest type was either open-cup or domed. Nests were placed at distances of 20 m, 200 m, and 400 m from the agricultural edge of east-central Illinois in 1991.

removed daily. Nest locations were changed (>20 m) for each trial. Rubber boots were worn to minimize scent trails.

Survival rates were estimated by calculating egg-days of survival (referred to as egg survival) and the number of predator-free days (referred to as nest survival) each nest experienced. For each nest, we determined egg survival by summing the number of days each egg remained in the nest undisturbed. Each nest could achieve a maximum egg survival of ten (four days for the first egg deposited, three days for the second egg, two days for the third egg, and one day for the fourth) if left undisturbed for the duration of the trial. Nest survival is defined as the total number of days in which the nest was undisturbed. Thus, each nest received a score between 0 and 4.

Data for both nest survival and egg survival were analyzed using an ANOVA. Tests were performed on untransformed data using general linear models (SAS 1990; PROC GLM). Main effects were nest type (two levels: domed and open-cup), distance from the forest/field edge (three levels: 20 m, 200 m, and 400 m), and date of trial (four levels: trials 1, 2, 3, and 4).

Results.—During this study, 172 of the 189 (91%) nests were disturbed at least one time. Whether using nest survival or egg survival, significant differences were found for all three main effects: distance from the edge, date of trial, and nest type. However, no interactions were significant (Table 1). All results for survival measures are based upon pooled data from the four trials and nest type when appropriate. Nests located 20 m from the forest/field edge exhibited significantly lower egg survival ($\bar{x}$ = 1.61 egg-days/nest) than nests located 200 m or 400 m from the edge ($\bar{x}$ = 2.63 and $\bar{x}$ = 2.89 egg-days/nest, respectively). Nests 200 m and 400 m were not statistically different from one another. Nest fate was also

associated with nest type. Egg survival was significantly lower for open-cup nests ($\bar{x}$ = 1.81 egg-days) than for domed nests ($\bar{x}$ = 2.94 egg-days), and this relationship was consistent at all three distances from the edge. Nests from trial 1 had a significantly higher egg survival than those of subsequent trials which were statistically indistinguishable from one another. Analyses performed using predation-free days exhibited identical significant relationships amongst the effects (Table 1) as those reported for egg survival.

No brood parasitism was recorded during the study. The lack of parasitism most likely reflects the tendency of Brown-headed Cowbirds (*Molothrus ater*) to locate their host's nest visually by following either parent back to the nest (Thompson and Gottfried 1981). The predators responsible for the extremely high predation rates recorded during this study were not identified.

Discussion.—Our results indicate a difference in predation rates for the two nest types used in this study. Domed nests, mimicking those built by Ovenbirds, had a significantly higher egg survival rate than did open-cup ground nests, typical of most other Neotropical migrants. This effect was seen regardless of the distance from the edge or for the trial period. Our results do not appear to be consistent with the literature (Martin 1992, Robinson 1992), which indicates Ovenbird egg survivorship to be very similar to that of other Neotropical migrants. Robinson (1992) did find that Ovenbirds had lower rates of brood parasitism, suggesting that domed nests may offer some defense against nest disturbance. Despite apparently higher nest survivorship and lower brood parasitism rates, other factors, including low pairing success (Linder 1992, Villard et al. 1994), may contribute to the apparent decline in Ovenbirds (Robbins et al. 1989).

We found egg survival to be significantly lower in nests located near the edge (20 m) than those located in the forest interior (200 m and 400 m). These results are consistent with those of Gates and Gysel (1978), Wilcove (1985), Wilcove et al. (1986), and Andrén and Angelstam (1988). Yahner and Wright (1985), however, recorded no difference between predation rates of artificial nests near the forest/field edge and those in the forest interior. This might be explained by the relatively short distance (50 m) they chose to define the interior.

The significantly higher egg survival rate we recorded during the first trial period has also been reported in several studies of natural nests (Zimmerman 1971, Dolbeer 1976, Best and Stauffer 1980). Subsequent decreased egg survival may result from an increase in the density of nest predators and the development of a search image that increases foraging efficiency (Bowman and Harris 1980).

The forest consisted of an open understory, few shrubs (DBH $<$ 7.5 cm), and almost no grasses. Several studies have shown that greater vegetational diversity and density reduce predator foraging efficiency (Bowman and Harris 1980, Sudgen and Beyersbergen 1986, Yahner and Cypher 1987). The lack of heterogeneity within the Boot may result in high predation rates throughout the forest.

Although our results suggest a higher nest survivorship near forest edge, predation rates upon all artificial nests were high throughout the study area. The results could be interpreted in several ways, depending on what scale and/or criteria are used to define edge (Paton 1994). Despite our own lack of resolution in this study, we support Paton's (1994) suggestion of increasing sampling effort within 200 m of the ecotone.

Acknowledgments.—We thank the Eastern Illinois Univ. Council for Faculty Research and the Champaign County Audubon Society for funding of this research. M. A. Villard reviewed the manuscript, and Roger Jansen and Yen-min Kuo provided field assistance.

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Wilson Bull., 107(1), 1995, pp. 174–178

Diet of nesting Killdeer in North Dakota.—The Killdeer (*Charadrius vociferous*) is one of the most widespread of all North American shorebirds and, unlike other shorebirds, tolerates a wide variety of open inland habitats in addition to the shores of coastal and inland water. Given its common status, there is surprisingly little information on the Killdeer diet. The only study is an unpublished report by Baldwin (1971) on their diet during the breeding season (June 16 to July 28) on the shortgrass prairie of eastern Colorado. Henderson (1927), Bent (1929), and Martin et al. (1951) also provide qualitative summaries of the Killdeer diet. Rundle (1982) compared esophageal and gizzard analysis in four species of shorebirds including Killdeer and found the three main taxonomic groups eaten by Killdeer were Coleoptera adults (40% occurrence), Diptera larvae (40%), and Coleoptera larvae (20%). No diet preference studies have been done on the Killdeer.

Because of concern for the impacts of pesticides on upland shorebirds, we conducted a study investigating the direct and indirect effects of carbaryl grasshopper control on Killdeer nesting on the U.S.D.A., Animal Plant Health Inspection Service (APHIS), Plant Protection and Quarantine (PPQ), Grasshopper Integrated Pest Management (GHIPM) demonstration site in western North Dakota. Killdeer gizzard analyses were performed to investigate a possible functional response in the Killdeer as a result of a reduction in arthropod availability caused by range grasshopper control. Killdeer were collected from areas sprayed with carbaryl Sevin-4 oil formulation and from similar unsprayed habitat. Each Killdeer was analyzed for brain acetylcholinesterase activity, pesticide residues (including organochlorines), whole body % lipids, and gizzard contents. Relative arthropod abundance was also estimated on the sprayed areas. Here, we report the gizzard contents of the Killdeer collected for this research and compare these data with the Killdeer diet reported by Baldwin (1971) which was also based on an analysis of gizzard contents. We also contrast the diet data with the arthropod abundance data to see if Killdeer exhibit any dietary preferences.

This study was conducted on two locations treated for grasshopper control by USDA, APHIS, during the summer of 1992. The first area (Towner area) was primarily on privately owned rangeland, located northwest of Towner in McHenry County, North Dakota. The mixed prairie vegetation of this area is dominated by needle-and-thread grass (*Stipa comata*) and western wheatgrass (*Agropyron smithii*). Small woodlands on the area included green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), quaking aspen (*Populus*

tremuloides), narrowleaf cottonwood (*P. angustifolia*), and wild rose (*Rosa acicularis*). Annual cereal grain production characterizes the interspersed cropland, with a small percentage devoted to hay production. The second area (Medora area) was approximately 240 km southwest of the Towner area and was primarily on the Little Missouri National Grassland (LMNG) south of Medora in Billings County. The vegetation is a mixed-grass prairie dominated by blue grama (*Bouteloua gracilis*), western wheatgrass, needle-and-thread grass, prairie junegrass (*Koeleria pyramidata*), and threadleaf sedge (*Carex filifolia*). The grasslands are dissected by woody draws that support some shrubs such as silver buffaloberry (*Shepherdia argentea*) and chokecherry (*Prunus virginiana*), and the principle trees are green ash, Rocky Mountain juniper (*Juniperus scopulorum*), and cottonwood (*Populus deltoides*) (Fowler et al. 1991). The LMNG is managed for multiple use, including grazing, and a significant percentage of the area is developed for oil and gas extraction, as nearly all of the region is underlaid by lignite coal. One untreated control area was located 10–17 km from each treatment area.

Killdeer were collected on treatment and control areas by shotgun June 22–July 29 1992, under the U.S. Dept. of the Interior, Fish and Wildlife Service Permit PRT-719665 and North Dakota State Permit 0125 (this research was approved by Colorado State Univ.'s Animal Care and Use Committee Protocol No. 92-150A-01). Most Killdeer were located around windmills and water holes, in grazed pastures, or in level short-grass habitat. Birds were sexed by internal examination and aged either to adult or juvenile by feather growth. Gizzard and esophagus contents were separated on foil and frozen in the field for analysis later in the laboratory. This facilitated prey item identification and minimized post-mortem digestion of food items which may occur in birds. Collected specimens were transported on dry ice from the field and then stored at −80°C. Wet weight of the gizzard contents was also measured while still frozen. Voucher prey items were collected from the field and various sources were used to aid the identification process (Borror and White 1970, White 1983, Chapman and Rosenberg 1991). Numbers of individuals within a sample could be counted based on the number of body parts (e.g., six beetle legs = one Coleoptera).

The relative abundance of ground-dwelling and flying arthropods on the two treated areas were estimated concurrently using pitfall traps. Pitfall traps were placed in a trapping web (Anderson et al. 1983). Each trapping web consisted of eight lines radiating out from a central point and each line had 10 traps each separated by 1.5 m (N = 80). This results in trap densities declining from 1.13 traps/m^2 at the center, to 0.01 traps/m^2 at the edge. Each trap consisted of three plastic cups (Baars 1979, Quinn et al. 1990). Traps were checked two days after installation and invertebrates were collected for identification.

Gizzard content variables were compared using two-way analysis of variance (ANOVA; PROC GLM) and significance for all analyses was inferred at the $P < 0.05$ level. (SAS Institute Inc. 1987). To evaluate diet preference, the proportions of Orthoptera, Coleoptera, and other arthropods (all remaining orders pooled together) in Killdeer diets and the proportions of the same three categories of arthropods caught in the pitfall traps were compared using a Chi-square goodness-of-fit test with a Bonferroni 95% confidence interval (Ott 1988).

A total of 72 Killdeer were collected (59 adults [38 males, 21 females], 13 juveniles). A total of 1501 prey items were identified; 96% of these items were identified to the family level (Table 1). The mean wet weight for the adult gizzard contents was 0.679 g ± 0.062 SE and 0.643 g ± 0.143 SE for juveniles. There was no difference in the gizzard weight between age classes ($F = 0.06$, $P = 0.809$). There was also no difference in the number of different prey families taken by adults and juveniles ($F = 0.04$, $P = 0.849$). Males and females did not differ in their gizzard content weight ($F = 3.58$, $P = 0.06$) or in the number of families consumed ($F = 0.03$, $P = 0.863$). Coleoptera were the predominant prey taken

Table 1

Diet (Mean Number of Individuals Per Gut and Percent of Total Gut Contents) of Killdeer from North Dakota[a] (This Study 1992) and Colorado (Baldwin 1971)

Taxonomic group	$\bar{x}$ ± SE	Percent of total[b]	Baldwin (1971) percent of total
Acrididae (short-horn grasshoppers)	5.97 ± 0.77	25.6	0
Gryllidae (crickets)	0.01 ± 0.04	0.1	5.0
Carabidae (ground beetles)	8.40 ± 0.34	26.2	33.0
Tenebrionidae (darkling beetles)	2.71 ± 0.53	8.5	26.3
Curculionidae (weevils)	2.35 ± 0.71	7.1	8.3
Scarabaeidae (scarabs)	2.21 ± 0.31	6.8	7.8
Hydrophilidae (water scavengers)	0.43 ± 0.20	1.3	13.3
Chrysomelidae (leaf beetles)	0.36 ± 0.19	1.1	0.3
Histeridae (hister beetles)	0.23 ± 0.23	0.7	0.9
Melyridae (soft-winged flower beetles)	0.03	<0.1	0
Ptinidae (spider beetles)	0.01	<0.1	0
Unidentified coleoptera larvae	3.1 ± 0.34	9.7	0
Dermestidae (dermestid beetles)[c]	0.13	<0.1	0
Dytiscidae (predaceous diving beetles)[c]	0.04	<0.1	0.3
Syrphidae (rat-tail maggots)	0.77 ± 0.91	3.3	0
Sarcophagidae (flesh flies)[c]	0.43 ± 0.85	1.9	0
Ptychopteridae (phantom flies)[c]	0.40 ± 0.76	1.7	0
Muscidae (muscid flies)[c]	0.06	0.2	0
Stratiomyidae (soldier flies)[c]	0.01	<0.1	0
Asilidae (robber flies)[c]	0.01	<0.1	0
Bombyliidae (bee flies)[c]	0.01	<0.1	0
Tabanidae (deer flies)	0.01	<0.1	0
Lepidoptera larvae	0.11	0.5	1.5
Hemiptera (unidentified)	0.03	<0.1	0
Corixidae (water boatman)	0.01	<0.1	0
Notonectidae (back swimmers)	0.01	<0.1	0
Hymenoptera (unidentified)	0.0	0.0	0.3
Halictidae (Halictid bees)	0.03	<0.1	0
Formicidae (ants)	0.56 ± 0.32	2.4	1.4
Aphididae (aphids)	0.03	<0.1	0
Trichoptera (caddisflies)	0.17 ± 0.10	0.7	0
Acarina (mites)	0.04	<0.1	<0.1
Hirudinea (leeches)	0.01	<0.1	0
Mollusca	0.0	0.0	0.4
Gastropoda (snails)	0.08	0.4	0
Bivalvia (clams)	0.01	<0.1	0
Plant material (seeds)	—	0.2	0.3

[a] Pooled from individuals collected at all four sites (two treatment and two control sites).
[b] % of total from 1509 total prey items identified.
[c] Larvae.

by Killdeer, occurring in 100% of the gizzards and ranging from 4–19 individuals per gizzard. Major beetle families (>5% of diet) included, in order of occurrence, Carabidae, Tenebrionidae, Curculionidae, and Scarabaeidae. Other important arthropod groups included Orthoptera (Acrididae), Coleoptera larvae, and Diptera larvae. Orthoptera (Acrididae) occurred in 63% of the gizzards, and the number of Orthoptera found per gizzard ranged from zero to 14. Grit was found in only a few samples. One sample contained both glass and a piece of aluminum. Two chicks less than two-weeks-of-age also were collected and their mean gizzard content weight was 0.093 g. The majority of the Killdeer chick prey was weevils (Curculionidae) and small carabid beetles. No grasshoppers were consumed by the chicks.

The major difference between these results and Baldwin's (1971) findings (Table 1) is the importance of grasshoppers in the diet. No grasshoppers were taken by the Killdeer (N = 4) in the eastern Colorado study, whereas grasshoppers comprised 25.6% of the prey items identified in the North Dakota gizzards. These differences are probably due to differences in the habitats of the two study areas and in grasshopper availability. The Killdeer in North Dakota were collected from grasshopper outbreak areas with an average of 17 grasshoppers/m^2 pretreatment which declined to 2–3/m^2 posttreatment (Fair 1993). Bent (1929) reviewed published food habits of Killdeer and reported heavy use of grasshoppers when abundant. Another major difference between the two study areas was the abundance of Diptera larvae in the Killdeer diet. Diptera larvae in our study constituted 7.2% of the total Killdeer diet but were not consumed by the Colorado birds. Darkling beetles (Tenebrionidae) were important prey in both study areas (26.3% in Colorado; 8.5% in North Dakota). Conversely, water scavengers (Hydrophilidae) comprised 13.3% of the Colorado diet and only 1.3% of the North Dakota diet. A total of 16 arthropod families were identified in Colorado and 31 families in North Dakota. These taxa differences may be due to (1) a higher availability of aquatic habitat on the Colorado site and (2) differences in sample sizes between the two studies.

There was significant difference in the proportions of the three prey groups, Orthoptera, Coleoptera, and other arthropods in the diet of the Killdeer and the available arthropods caught in the pitfall traps ($\chi^2 = 6669$, $P < 0.001$). Orthoptera use fell within the Bonferroni 95% confidence interval for the expected proportion, Coleoptera was lower than the confidence interval, and other arthropods were above the interval. These results suggest the Killdeer exhibited a diet preference in this study. Preference, in this case, refers to a greater proportion of one of the three groups of prey used in a greater proportion of that group available on this study area. The major difference was the percentage of Coleoptera taken by the Killdeer (52%) which was greater than the percentage found in the pitfall traps (5%). The birds took Orthoptera in proportion to their availability. Due to the fact that both sampled locations were grasshopper outbreak areas and were selected for grasshopper control, Orthoptera can be considered an abundant resource. Hence, Killdeer were foraging opportunistically on a more available food resource.

Acknowledgments.—We acknowledge the help of Rachael Miller, for assistance in the field, and Brett Petersen and Orrin Myers for help in data analysis. We also thank Robert Cook and Walter Graul, for help in study design, and Boris Kondratieff for identifying unknown arthropods. Support for this project was provided by the U.S. Department of Agriculture APHIS-PPQ Grasshopper IPM Project.

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Wilson Bull., 107(1), 1995, pp. 178–179

Unusual Marbled Murrelet nest.—Marbled Murrelets (*Brachyramphus marmoratus*) nest primarily in trees, except in treeless or nearly treeless areas of Alaska where they are known to nest on the ground (Mendenhall, Proc. West. Found. Vertebr. Zool. 5:5–16, 1992; Piatt and Ford, Condor 95:662–669, 1993). We observed a ground-level Marbled Murrelet nest in old-growth forest in July–August 1993. The nest was located in the Log Jam Creek drainage of northern Prince of Wales Island in southeastern Alaska (55°52′56″N, 132°57′53″W). Southeastern Alaska contains the greatest numbers of Marbled Murrelets in North America (Mendenhall 1992, Piatt and Ford 1993).

On 23 July, H. Lambert found a clifftop nest containing an egg. On 27 July this nest was occupied by an adult Marbled Murrelet incubating a single pipping egg. After approximately

3 min, a Marbled Murrelet flew to the nest when Ford was 3–4 m away. On 28 July, an adult Marbled Murrelet flushed from the nest as we approached. The pipping egg was rocking in the nest. We set an 8 mm video camera near the nest to record the adult's return and departed at 05:12. At 05:17, an adult Marbled Murrelet landed at the platform and approached to within 10 cm of the egg. It sat almost motionless, near the egg, until flushing at 05:29 upon our approach. Approximately 2 min later, before we could leave the nest site, the adult flew to within 1 m of the nest before flying away again.

On 2 August, Ford found the nest unattended. Eggshell fragments were located at the foot of the cliff below the nest. Absence of a nestling, the condition of the eggshell fragments, and the lack of fecal material in the nest suggested that the egg (or nestling if it hatched) had been destroyed by a predator. The persistent behavior of the adult Marbled Murrelet(s) around the nest while we were present in the area indicated that it probably did not abandon the nest until the egg (or nestling) was destroyed.

The nest was on a platform of moss (*Hylocomium splendens* and *Rhytidiadelphus loreus*) on top of three intertwining roots of a western hemlock (*Tsuga heterophylla*), 26.7 cm in diameter at breast height (dbh) and approximately 15 m tall, at the top edge of a cliff. The nest platform was suspended 11 m above the foot of the cliff. The nest platform was 65 cm × 35 cm and 4 cm deep with no evidence of nest construction. The tree was on a west-facing (260°) 38° slope, at 195 m elevation. The bird(s) departed from and approached the nest on the down-slope side of the cliff (245°), and we observed one possible landing pad on this side, a worn area on a moss-covered root about 40 cm from the nest. The tree was approximately 13 km from the nearest salt water in an old-growth, uneven-aged stand of western hemlock-western red cedar (*Thuja plicata*). The mean dbh of the trees (>2.5 cm dbh) within a 25-m radius plot was 23.6 cm (SD = 20.4, range = 2.5–114.3 cm, N = 184). The primary ground cover plants were menziesia (*Menziesia ferruginea*) and blueberries (*Vaccinium alaskaense* and *V. ovalifolium*). This nest was unusual because it exhibited dual nest placement characteristics (ground and tree). When approached from up slope, it was at ground level, although the platform was on tree roots. When approached from down slope, it appeared similar to more typical Alaskan tree nests in that the nest platform was >10 m above the ground. The characteristics of the platform and nest cup were also similar to other tree nests in Alaska (Naslund et al., unpubl. data). We know of four other intact Marbled Murrelet eggs that have been found on the ground in forested habitats. Two (UWBM 43098 and UWBM 43031) were found on Long Island, Washington, and appeared to have fallen out of tree nests or have been moved by predators (J. Atkinson, pers. comm.). Two were found on Prince of Wales Island in 1993, one in an open muskeg (M. Minnillo, pers. comm.) and the other along the edge of a tributary of the Thorne River (S. Seaford, pers. comm.). It is not known whether either of these eggs came from ground or tree nests.

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Wilson Bull., 107(1), 1995, pp. 179–181

The parasitic blow fly, *Protocalliphora spatulata*, in two new host species.—Larvae of the parasitic blow fly *Protocalliphora spatulata* (Diptera: Calliphoridae) were found on two new host species, Savannah Sparrows (*Passerculus sandwichensis*) and White-crowned Sparrows (*Zonotrichia leucophrys*) during the summers (25 May to 25 July) of 1990–1993

on the Delta Agriculture Project (44,500 ha) located south of the Tanana River approximately 150 km east of Delta Junction, Alaska (64°00′N, 145°20′W). The area is a mosaic of different-aged small grain and hay fields cleared from the surrounding forest of black spruce (*Picea mariana*), white spruce (*P. glauca*), and aspen (*Populous tremuloides*). Cereals (mainly barley), grass seed, and hay are the primary crops grown in this area. Approximately 8900 ha of the project is currently in agricultural production. The majority of the area (35,600 ha) is idle or in government set-aside programs. Vegetation on the idle and set-aside sites is comprised of a variety of grasses (*Calamagrostis* spp., *Agropyron* spp., *Festuca* spp.) and forbs (*Epilobium* spp.), interspersed with willow (*Salix* spp.) and aspen (*Populus* spp.) windrows.

Sparrow nests were located by flushing the adults from their nests and were visited daily until the first egg hatched (day 0), and then revisited four and seven days later. Nestlings were banded under U.S. Fish and Wildlife Service Permit Number 20819. Larvae often were removed from the sparrows, or fell off when handled, and were reared to adults for identification. Specimens were deposited in the C.P. Gilette Museum of Arthropod Diversity at Colorado State Univ. Larvae were found on 43 of 395 Savannah Sparrow nestlings over four years. The percent of parasitized Savannah Sparrow nests was 17.9% (N = 28) in 1990, 25.7% (N = 35) in 1991, 31.4% (N = 35) in 1992, and 63.3% (N = 16) in 1993. Parasitized nests contained an average of 66% (SE = 5.7) parasitized nestlings. Most parasitized nestlings were seven days old and the blow fly larvae were often fully developed by the time the young fledged, typically at nine days post-hatch. Larvae were most often found on the wings (48% of 189 larvae) but were also found on the face (21%), body (13%), head (7%), legs (5%), feet (3%), back (2%), and neck (1%). The average parasite load per individual parasitized Savannah Sparrow was 2.9 (SE = 0.29, range 1–10). In 1993 three dead Savannah Sparrows were found in one nest on the seventh day after hatching. A total of 41 *P. spatulata* larvae were collected from the three nestlings. Only five White-crowned Sparrow nests were found during 1990–1993. However, 100% of the nestlings were found to harbor *P. spatulata* larvae. White-crowned Sparrows also nest on the ground, concealed by vegetation (Harrison 1978); however, they typically were associated with the forest edge on our study site.

P. spatulata is distributed from Alaska to western Ontario and south to California and New Mexico (Sabrosky et al. 1989). It is found chiefly at high elevations, typically in rocky alpine tundra. However, the nearest tundra habitat is over 50 km from our study site. *P. spatulata* has only three previously reported hosts; Horned Larks (*Eremophila alpestris*) (Verbeek 1967), American Pipits (*Anthus rubescens*) (Verbeek 1970), and Rosy Finches (*Leucosticte arctoa*) (Sabrosky et al. 1989).

Similar to *P. braueri, P. spatulata* larvae produce myiasis by burrowing into the subcutaneous tissue of the host. In other *Protocalliphora* spp., this habit can lead to substantial host tissue damage (Howe 1991). However, *P. hirundo* is the only member of the genus confirmed to be an obligate subcutaneous parasite and has also been found in Savannah Sparrows (George and Mitchell 1948, Bedard and McNeil 1979, and Garrison et al. 1986).

Acknowledgments.—We appreciate the assistance of B. Kondratieff for identifying the blow fly specimens. Earlier versions of this manuscript benefited by comments from L. C. McEwen, F. P. Howe, and two anonymous reviews. Support for this project was provided by U.S. Dept. of Agriculture APHIS-PPQ Grasshopper IPM Project.

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Wilson Bull., 107(1), 1995, pp. 181–182

Fruit in the diet of nestlings of the Puerto Rican Tody, a tropical insectivore.—Many tropical frugivorous birds supplement the diet of their nestlings with insects, particularly in the early stages of development (Lack 1968, Skutch 1969, Morton 1973). In some of these cases, the nestling diet is exclusively insects (e.g., Skutch 1944). Although some frugivorous birds feed their young entirely on fruit as well (e.g., D. W. Snow 1962, B. K. Snow 1970), the growth rates of chicks of such species are relatively slow (Ricklefs 1976). Fruits are generally low in nutritional value, and the supplemental use of insects high in protein may enable tissue growth to proceed more rapidly (Morton 1973, Ricklefs 1976, Reinecke 1979). The opposite case, of birds which are insectivorous as adults feeding fruit to nestlings, is extremely unusual (Morton 1973) although not undocumented (e.g., Ligon 1970). Here I report observations of a tropical insectivorous bird, the Puerto Rican Tody (*Todus mexicanus*), supplementing the insect diet of its nestlings with fruit.

I observed (through binoculars) a pair of Puerto Rican Todies feeding nestlings from 8 July to 16 July 1993 in the Maricao Forest Reserve, Puerto Rico (18°09′N, 67°00′W). The nest was a burrow beneath the roots of a tree in an embankment. I report here only feeding observations which I was able to record for at least 30 min without interruption, for a total of 7.5 h. Due to the abrupt angle of the tody's nest burrow, I was unable to determine either the number or age of the nestlings.

As adults, todies are wholly insectivorous, and Kepler (1972) reports an exclusively insectivorous diet for the nestlings as well. In my observations at the nest in Maricao, the majority of the food items brought appeared to be either lacewings (Neuroptera) or moths (Lepidoptera). However, 30 of the 163 feedings I witnessed (18.4%) consisted of a single type of fruit, the small, bright orange fruits of a tree, *Clusia krugiana* (Guttiferae). During my observations, these trees were in full fruit, and many other species of birds I caught during the same time period showed evidence of having recently eaten the same fruits. The

todies brought the *Clusia* fruits to the nest on at least one visit during every observation period over the span of 7.5 h.

I identified the parent by color bands in 150 of the 163 feedings observed. The female P162 fed the nestlings significantly more frequently than the male R158 ($\chi^2 = 5.23$, df = 1, $P = 0.02$); however, the male brought fruit to the nestlings significantly more frequently than did the female ($\chi^2 = 4.17$, df = 1, $P = 0.04$). Overall, the todies averaged 21.7 feeding visits per hour, greater than the 10.8 visits per hour average reported by Kepler (1972). Kepler reports a significant increase in the frequency of feeding as the chicks approach fledging; it may be that the nestling todies at this nest were close to fledging, but I was unable to determine whether this was the case.

Acknowledgments.—I thank the Puerto Rico Dept. of Natural Resources, for allowing me to conduct research in their system of State Forest Reserves, and particularly the staff of the Maricao Forest Reserve for their kind assistance. This work was supported in part by a field research grant from the Univ. of New Mexico Latin American Institute, a grant from the Graduate Research Allocations Committee, Dept. of Biology, Univ. of New Mexico, and a grant from the Student Research Allocations Committee of the Graduate Student Association of the Univ. of New Mexico. J. D. Ligon and P. W. Zwartjes provided helpful comments on the manuscript.

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Wilson Bull., 107(1), 1995, pp. 182–184

Notes on the nesting behavior of the White-bellied Woodpecker.—This note provides new information on the nesting behavior of the White-bellied Woodpecker (*Dryocopus javensis*) on the island of Mindanao in the Philippines. A team of biologists from the Field Museum of Natural History and several institutions in the Philippines studied the vertebrates

of Mt. Kitanglad, Bukidnon Province, Mindanao, Philippines, between 700 and 1850 m above sea level from 16 April to 22 May 1992. Camps were established at 1100 m in primary lowland rain forest and at 1600 m in primary montane rain forest. White-bellied Woodpeckers were sighted on 12 of the 16 (75%) days of observation at the 1100 m camp in primary lowland rain forest and on three of the 24 days (12.5%) spent at the 1600 m camp in primary montane rain forest but were not detected in transitional montane/mossy forest on higher ridges. Other species of woodpeckers known from the mountain are the Greater Golden-backed Woodpecker (*Chrysocolaptes lucidus*) and the Philippine Pygmy Woodpecker (*Picoides maculatus*), both of which were seen occasionally at both camps.

On 27 April 1992, an active White-bellied Woodpecker nest was discovered in a dead tree trunk on one side of the ridge on which the 1100 m camp was located. The nest was in a 25 m tall dead trunk of about 80 cm dbh, with the nest hole 1 m below the tip of the trunk about 4 m above the level of the ridgetop. The ridge was oriented more or less in a north-south direction, and the nest hole faced approximately northwest. The hole had been checked on several occasions prior to 27 April, suggesting that either the two nestlings were not reaching the nest entrance, or were doing so less frequently. We established a blind on the ridgetop about 30 m from the nest hole and accumulated 15.25 h of daylight observations between 0500 and 1800 h on 28–30 April.

The two nestlings spent much of the day with their heads and necks extended out of the nest hole. Because their bodies clearly filled much of the upper nest cavity, access to the outside was accompanied by considerable pushing and shoving. An adult woodpecker was seen to visit the nest at least eight times during observation periods on those three days, usually arriving out of sight lower on the nest trunk, hitching up to the nest hole and always accompanied by active begging by the nestlings. On three of these visits, the adult fed the nestlings, with the nestling placing its bill inside the adult's throat to receive the regurgitated food. At least one of the feedings involved multiple deliveries of food—six times to one nestling and once to the other. Surprisingly, adults were not seen to carry away any fecal matter. The degree to which the presence of our blind influenced the frequency of nest visits or whether or not young were fed in unclear. Although two adults were frequently heard calling in the vicinity of the nest, only one individual was ever seen on the nest trunk at one time, and in all cases, this individual was a female by plumage. Observations terminated on 1 May with our departure; however, the nest cavity was apparently unoccupied during brief checks on 5 and 21 May, suggesting that our observations were of nestlings almost ready to fledge.

The information accumulated on White-bellied Woodpeckers during our observations on Mt. Kitanglad fits well with that summarized by Short (*Woodpeckers of the world,* Delaware Museum of Natural History, 1982), especially in the timing of nesting and the characteristics of nests. Although males apparently do much of the excavation of nest cavities, and both adults seem to participate in incubation of eggs, no information has been available regarding adult behavior during the nestling and fledgling stages in this species. Our observations indicate that the female may do the bulk of the feeding of nestlings, suggesting an interesting mix of collaboration and division of labor between the sexes in White-bellied Woodpeckers.

Acknowledgments.—We thank our field companions for their interest, patience, and support during this brief study, most especially L. R. Heaney who organized and directed the expedition. Peterson thanks R. M. Salazar S. for her friendship and support throughout. Permits for this research were provided by the Protected Areas and Wildlife Bureau of the Dept. of Environment and Natural Resources, Philippines. Funding was supplied to L. R. Heaney by the MacArthur Foundation.

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Wilson Bull., 107(1), 1995, pp. 185–191

ORNITHOLOGICAL LITERATURE

Restless Energy—A Biography of William Rowan. By Marianne G. Ainley, Véhicule Press, Montréal, Canada. 1993:368 pp., colored cover, 22 illustrations including black-and-white photographs, manuscript pages, and art work. $19.95.—Over the years when I lectured in ecology and ornithology classes about the effect of light on birds, I would mention "someone's" experiments exposing juncos in Canada to increasing lengths of artificial daylight in autumn to see if the birds would fly north. Both I—and presumably the students—viewed this as (1) a clever endeavor and (2) worthy of a chuckle. But did some scientist really try this? Or was it only apocryphal? In the pages of "Restless Energy" came the revelation, not only about this but many other of my lecture topics, as the life work of the remarkable European-born Canadian biologist William Rowan unfolded.

The lad of ten (in 1901) who carried, in a tea infusion ball, "migrating French flies to England" would proceed, over his lifetime (he died in 1957), to do classical studies on the mechanism of migration, the effect of light duration on juncos, crows, and other species, light and seasonal reproduction in animals, the role of hormones in bird behavior, wildlife population cycles (it was Rowan who originally proposed the famous snowshoe hare/lynx research), and ecological studies of waterfowl and other vertebrates.

Biographer Ainley was aware of these accomplishments through her work on a history of Canadian ornithology. But was there more to this Rowan than met the scholarly eye—a life worthy of a biography? From letters, diaries, interviews, and junkets, there emerged the framework for "Restless Energy," the reflections on a man who not only did imaginative research in field and laboratory but taught biology, shaped Canadian zoology departments, sketched and painted (his art became collectors' items), wrote scientifically and popularly and provided a voice for nature on the new medium of radio, vexed over endangered species and promoted the idea of wildlife refuges, led field excursions, gave public lectures, became involved in later life with social issues, concern for the environment, and world overpopulation, throughout his career inspired students who would become important in their own right, and even received permission to shoot starlings from the roof of the National Gallery in downtown London. Sadly enough, his wife and growing family increasingly faded into the background of this busy man.

In seventeen chapters, Marianne Ainley takes Rowan from his beginnings (Chapter 1: "The Lap of Luxury, 1891–1908") to his finale (Chapter 17: "Science, War, and Ethics: a Biologist Looks Forward"), with a retrospective epilogue. The selection of illustrations portrays his family, the scientist himself over his life span, historic research events (such as the "airliners" for crows) and manuscripts, and some of Rowan's own delightful artistry. Indeed, the frontispiece is his sketch of Slate-colored Juncos, but personally I would have preferred, facing the title page, Rowan's 1916 self-portrait, out in the field relaxing on a folding stool, in knee pants, knee socks, and tie, collecting gun in hand, a cigarette between two fingers, and sketch pad and pencil on the ground nearby. Incidentally, included with Ainley's biography are extensive footnotes, Rowan's own lengthy bibliography, and publications about him.

Was it the Canadian border that kept me from ever mentioning Rowan in class? We must indeed be provincial, because I don't remember ever having noted him. It surprised me, then, to discover how widely known he was, a compatriot of Charles Elton, Allan Brooks, Ernest Thompson Seton, Joseph Grinnell, W. C. Allee, Julian Huxley, A. C. Bent, Thomas Barbour, Francis Harper, Percy Taverner, the Hamerstroms, Konrad Lorenz, Niko Tinbergen, Albert Wolfson, and Donald Farner, to drop some names. Surely there haven't been many other professional ornithologists who were highlighted in "True" magazine.

Rowan's was, indeed, an energetic life, though restless and not always happy. Ainley has provided the full spectrum, some interesting, some dull, from excitement with innovative research and the relaxation of a wilderness excursion to administrative and personal conflicts and depression over the state of the world. Now that I know this indefatigable field man, I warm to Thornton Burgess' toast delivered at the 1931 Metamek Conference on wildlife cycles: "May Rowan's birthdays attain their peak only when all the crows fly north." I'm glad I never told my classes that the juncos indeed flew north, seeking an eternal spring in the fall. For in actuality they never did, though Rowan must secretly have hoped they would.—Richard G. Beidleman.

The Birds of Africa. Volume IV. Stuart Keith, Emil K. Urban, and C. Hilary Fry. Color plates by Martin Woodcock; line drawings by Ian Willis. Acoustic references by Claude Chappuis. Academic Press, London. 1992:609 pp., 32 color plates, two black-and-white plates, 359 range maps, and numerous line drawings. $145.00.—What began in the late 1970s as a labor of love by several devoted ornithologists with deep interests in African birds has since expanded into a research and writing project of greater magnitude than they had planned. Originally projected as a four volume treatise on Africa's avifauna, it has now expanded to seven. Volume IV is devoted to passerines, as will be the final three.

The authors had earlier assumed that more is known about Africa's large birds (approximately 800 species) than its passerines (roughly 1200 species). This proved not to be the case since their research revealed that the body of knowledge of African passerines is greater than they had supposed. It was this discovery which will require additional volumes to cover Passeriformes comprehensively.

To recap this enormous project: Volume I (Leslie H. Brown, Emil K. Urban, and Kenneth Newman), 1982, covers Struthioniformes to Falconiformes with an excellent introductory chapter on Africa's geological past, climate, ecosystems, habitats, bird migration, and research; Volume II (Emil K. Urban, C. Hilary Fry, and Stuart Keith), 1986, covers Galliformes through Columbiformes; Volume III (Fry, Keith, Urban), 1988, Psittaciformes through Piciformes; and Volume IV (Keith, Urban, and Fry), 1992, Passeriformes, including broadbills, pittas, larks, swallows, martins, wagtails, pipits, longclaws, cuckoo-shrikes, bulbuls, waxwings, Gray Hypocolius (*Hypocolius ampelinus*), silky flycatchers, dippers, wrens, accentors, and thrushes. Keith, Urban, and Fry have edited volumes II-IV with rotating senior editorship, a policy which is to continue through completion of the project.

Volume IV contains approximately 300 species accounts, as will each of the remaining three volumes. Individual accounts have been lengthened from 750 words to 1000 words, in most part due to expanded knowledge of Africa's birds. In addition to scientific names, common English and French names are provided and indexed for each species. Much of north and west Africa is Francophone, and while the text is not in French, this feature provides an element of accuracy in location of species for French-speaking readers. A spot-check of the extensive index of scientific, French, and English names turned up no errors.

The text is beautifully formatted. Although it is written partly in telegraphic fashion, it nevertheless is easy to read and reference. A comprehensive bibliography is structured in three sections: general and regional references, taxonomic family references, and acoustic references. The second section distills the salient literature for each family dealt with in Volume IV. Assembling this bibliography from the African region is no mean feat in itself.

Martin Woodcock's color plates are superb. They are more true-to-life when compared to earlier efforts of Volumes I and II. All color illustrations are presented on unadorned white textured background, standard in Volumes II–IV, a considerable improvement over several

pastel-backgrounded plates in Volume I. Ian Willis' line drawings are delightful and informative, and they serve a real purpose in illustrating behavioral aspects and anatomical features. The book's printing, color separation, and binding are of the highest quality and are in the finest tradition of Academic Press publications.

David A. Bannerman published the two-volume handbook set "The Birds of West and Equatorial Africa" in 1953. C. W. Mackworth-Praed and Captain Grant published a six volume handbook set on the birds of Africa (two volumes each for East Africa, Southern Africa, and West Africa) over a 20 year span from 1953 to 1973, but this work did not cover North Africa. These efforts, highly laudatory, are either incomplete or out-of-date. All have become collectors' pieces. "The Birds of Africa" fills an ornithological literary void in covering the entire continent.

One can only admire the intellectual energy and scholarly tenacity of the authors of The Birds of Africa considering the scattering of Africa's ornithological literature in many languages, published in a variety of local, national, and international journals, many of them obscure. When one thinks of the sheer enormity of this project, the beauty and accuracy of the result earns this volume and volumes I–III unusually high marks. The authors are to be warmly congratulated on their exceptional effort. In every way their work complements the diverse and fascinating panorama of African birds of which they so carefully write.

This volume, the first three, and the volumes yet to be published should be permanent reference fixtures in all university libraries where ornithology is taught or researched. "The Birds of Africa," destined to be an international ornithological classic, is a requirement for anyone who is seriously interested in African avifauna.—Larry Schwab.

The Downy Waterfowl of North America. By Coleen H. Nelson. Illus. by the author. Delta Station Press, Delta Waterfowl Foundation, Deerfield, Illinois, and Delta Waterfowl Research Station, Delta, Manitoba, Canada. 1993:302 pp., frontispiece and nine plates in color with captions, 92 black-and-white figures with captions or annotations, numerous black-and-white sketches throughout the text, and three appendices. Cloth $39.95 (plus $5.00 shipping per book) in U.S., $49.95 (plus $5.00 shipping per book) in Canada.—This is a beautiful and valuable book representing a lifetime of work illustrating and analyzing characteristics of the newly hatched, downy young of North American waterfowl (Anseriformes). Despite its coffee-table attractiveness resulting from beautiful as well as accurate color portraits of cygnets, goslings, and ducklings in lifelike positions, it is a thorough, precise, and serious scientific work. Six pages of acknowledgements read like a "Who's Who" of waterfowl enthusiasts, and represent a major effort to determine precise facts and double-check the results. The book format involves chapters covering Introduction, Materials and Methods, and Results, followed by tribal treatments, Discussion, and a lengthy and thorough reference section. Not all headings are in the table of contents, however, and variance in size and style of type used to denote first-order headings does create some confusion.

The objectives of this major effort clearly shifted over time from a series of illustrations by a fine artist documenting characteristics of day-old young to more scientific interests clarifying patterns of importance in identification and evolution. Comments early in the text point out the influence of her observations on acceptance and use of taxonomic categories and sequence. Most tribes follow the American Ornithologists' Union Check-list of North American Birds (1983) except for the addition of the Somateriini for the eiders between the pochards (Aythyini) and sea ducks (Mergini). Choice of generic names differs more, with *Anser* used in place of *Chen* for the white Arctic geese, and *Olor* in place of *Cygnus* for the native Nearctic swans. Earlier generic names such as *Philacta canagica* (Emperor

Goose), *Mareca americana* (American Wigeon), and *Nomonyx dominica* (Masked Duck) are resurrected partly because of the plumage patterns of downy young, and supporting documentation from anatomy or genetic analysis is cited. Information and viewpoints are a positive stimulus to rethink again anseriform taxomony.

The Materials and Methods section outlines the precise, Munsell-based color system used in the descriptions and in the special appendix that details colors documented during the author's studies. Justification for the concerted effort to use live rather than museum specimens includes representation of accurate colors and the correction of some long standing errors in the literature. Behavior and vocalizations of newly hatched young were recorded for many species, often using captive-reared birds. Geographic area of coverage is broad, including Greenland to the Aleutians, south to Hawaii and Columbia, and east to the West Indies. Thus, species like Barnacle Goose (*Branta leucopsis*), Pink-footed Goose (*Anser brachyrhynchos*), Laysan Duck *Anas laysanesis*), and White-faced Whistling Duck (*Dendrocygna viduata*) are illustrated, but marginal tropical species like the Comb Duck (*Sarkidiornis melanotus*) of Panama are not. Procedures for the weights and measurements are presented in the massive appendix table.

The Results section provides generalizations about plumage patterns, structure, vocalizations, and behavior. This is followed by sections of species- and sometimes subspecies-level treatment of the nine recognized tribes. Nine color plates are the core of this treatment, and all species are figured, including multi-color variants or phases of numerous species, many of which have not been illustrated before. The sequence of species presentation in the plates is generally taxonomic but varies due to design and spatial requirements for the plates. One plate considers subspecific variation in one species (Canada Goose, *Branta canadensis*), and other plates include as many as 11 species. Each description includes comments on general color patterns, "unfeathered parts," structural features, and, sometimes, behavior and vocalizations. A few species treatments cover subjects relating to adults, but generally the focus is solely on downy young. The Discussion considers issues of taxonomy and phylogeny, often at a worldwide level, and various biological and methodological problems that require interdisciplinary effort in the future.

Considering the 10 color plates, abundant black-and-white illustrations, and general layout and printing quality, the book is a bargain, and many will buy it for its attractiveness as well as its subject matter. The book is essential for all interested in the biology, taxonomy, evolution, and identification of waterfowl.—Milton W. Weller.

The Mississippi Kite. By Eric G. Bolen and Dan Flores. Univ. of Texas Press, Austin, Texas. (The Corrie Herring Hooks Series, No. 25). 1993:128 pp., one black-and-white and 15 color photos, most with captions, one black-and-white fig., two range maps, two tables, three appendixes. $ 17.95.—This is an enjoyable book; it transcends the usual tiresome and sterile reading of life history data. Two chapters in particular (covering 30 pages) make this book delightful. One chapter deals with the Mississippi Kite (*Ictinia mississippiensis*) in History and the other with Conservation and Management. The History chapter has four sub-sections: (1) Western Exploration and Discovery of the Mississippi Kite, (2) In the Southern Wilderness; Wilson, Long, and Audubon, (3) The Pacific Railroad Surveys and After, and (4) Mississippi Kites and Twentieth-Century Environmental Change. Section titles give an excellent idea of their content. The detective work behind the information is stimulating. For example, while the kite's scientific diagnosis and naming is credited to Alexander Wilson in 1811, it was actually discovered the first described (without being given a name and accompanying Latin description) following the 1806 expedition to the Red River.

The results and findings of that survey, however, were largely overshadowed by the seemingly more glamorous Lewis and Clark expedition, and thus the report of the Red River expedition was delayed in publishing. Only 200 copies were ever produced. The naturalist of the Red River expedition was Peter Custis, discoverer of the kite. He commented on his apparently subadult specimen (the would-be type specimen) as "A species of *Falco* which I have not seen described" and then gave a very exacting description but only in English. Too bad he did not follow the rules of nomenclature of the day and so was robbed of the privilege of naming a new species. The above events give a favor of the interesting material covered. The chapter on Conservation likewise has four sub-sections: (1) Kites in Cites, (2) Predators and People, (3) Winter Problems, and (4) Protected Areas. This chapter, in addition to discussing contemporary problems such as DDT and landscape alterations, also reviews historical aspects.

The bulk of the book (some 100 pages) covers standard life history information with chapters on Breeding and Nesting, Raising Young, and Food and Feeding. There is an extensive literature reference with 106 citations. In the introductory chapter a lengthy discussion, revolving more or less around two range maps, treats in good detail the changing nature of the species distribution and status. This chapter complements nicely Appendix C which reviews the past decade of sightings state by state. The Mississippi Kite is a species that has benefited in this century from more recent habitat alterations, having even moved into urban settings. The pre-1980s data relative to distribution and occurrence is treated in less detail and scattered throughout the book. There are delightful discussions of sexual size dimorphism, diets and helpers at the nest. Unfortunately, the treatment of size dimorphism largely limits itself to the hypothesis of food habit relationships as a driving force for size dimorphism (gender size differences are slight in raptors that feed on slow, easily caught food and dimorphism increases and is greatest in raptors that feed on agile, hard to catch food). Only lip service is given to the many other theories and especially the currently more favored and compelling sexual selection and female dominance ideas to explain the reversed sexual size dimorphism of raptors. Kin selection and the role of juvenile plumaged birds in nest helping is described and in fact helpers, which occurred at 17% of a sample of 209 nests, are mainly yearlings.

This book is well-written, easy to read, and contains new information with some provocative discussions. The price is hard to beat in today's market, and I highly recommend it even for non-raptorphiles.—Clayton M. White.

A Century of Avifaunal Change in Western North America. By Joseph R. Jehl, Jr. and Ned K. Johnson (eds.). Studies in Avian Biology 15, Cooper Ornithological Society. 1994:348 pp. $40.00.—One of the events celebrating the centennial of the Cooper Ornithological Society was a symposium on the topic "A century of avifaunal change in western North America." The present book contains the papers presented at that symposium. There are 26 papers grouped in five sections including (1) regional avifaunal change, (2) population trends of major groups of birds, (3) the effects of human-induced environmental change on avian populations, (4) case histories, and (5) prospects.

This is an important book containing numerous papers making noteworthy points. For example, the decline of Neotropical migrant birds seems to have been less in western United States than in the east. Analyses of regional change provide some specific examples of local increases and expansions as well as declines. The section of population trends includes studies that indicate both positive and negative changes in bird populations—waterfowl populations may be seeing better days, raptors are showing mixed responses to habitat

alterations, and population trends of landbirds are complex, to say the least. For example, Desante and George analyze population trends of landbirds and demonstrate that over the past 13–26 years, 58 species of migratory landbirds have decreased, 44 have increased, and 35 showed no change. The book is essential reading for students of North American bird populations.—C. R. Blem.

White Ibis: Wetland Wanderer. By Keith L. Bildstein. Smithsonian Institution Press, Washington, D.C. 1993. 272 pp., 23 b/w photos, 44 line drawings. $22.50.—This is not, as the title might imply, a summary and discussion of all that is known about the White Ibis. Rather, it is a personalized summary of the author's research on American White Ibises in South Carolina. It offers a nice overview under a single cover of the author's diverse research on the species. His research has ranged from physiology to breeding biology and foraging ecology to the ibis' place in the community.

This is a popular book as suggested by the non-technical style. The text is easy to read. Technical terms are avoided, and the few that are used are explained in easily understood every day English. The topics and research questions such as the evolutionary significance of coloniality of birds are discussed briefly and simply without going into great detail. References are cited in the text but not so frequently as to get in the way of easy reading. At the same time, the citations are adequate to lead the reader through the quite complete reference section at the back of the book to most of the scientific literature dealing with White Ibises.

The book begins with a summary of two ibises closely connected to human history: the Sacred Ibis (*Threskiornis aethiopicus*) and Waldrapp Ibis (*Geronticus eremita*). The discovery and misidentification of the American White Ibis by early North American ornithologists focuses attention on the main topic. The book then launches into the overview of the author's research. Chapters include the study area on Pumpkinseed Island in northern coastal South Carolina, breeding biology, colonial nesting, growth and development, feeding behavior, habitat use, salt stress and prey choice, ibises in ecosystems, and the affects of Hurricane Hugo on the colony. Each chapter is thorough. Information is presented as well as evolutionary questions: e.g., why do ibises nest colonially, why are the young dark and the adults light in color, etc.

One of the most important results of this research is the finding that the salt gland of nestling ibises is largely undeveloped so that the young cannot physiologically handle the stress associated with salty prey that adults can eat with impunity. The young become dehydrated. While adults feed for themselves largely on fiddler crabs in salt marshes near the breeding colony, they travel to inland freshwater wetlands to catch crayfish which they feed to their young. This is more than a merely interesting observation. It has large implications for habitat needs and conservation. This is brought home in two chapters on conservation. Ibises nesting in estuaries along the coast require freshwater habitats to ensure a supply of unsalty food for their young. Otherwise the birds cannot breed successfully. A case in point is that of the Scarlet Ibis, considered by many to be conspecific with the White Ibis, in Trinidad. While the ibises still inhabit the island, they have not bred there since 1970. The Caroni Swamp, where the birds had previously bred, has deteriorated with influx of salt water. The loss of the freshwater habitat has coincided with the birds' cessation of breeding in the area.

The book was very pleasant reading as well as thorough and informative. I fully recommend this to professional as well as amateur ornithologists and laymen who have an interest in these birds and their habitat.—Malcolm C. Coulter.

The New Atlas of Breeding Birds in Britain and Ireland; 1988–1991. Compiled by David Wingfield Gibbons, James B. Reid, and Robert A. Chapman. British Trust for Ornithology, Scottish Ornithologist's Club, and Irish Wildbird Conservancy, T & A D. Poyser, London. 1994:xiv + 520 pp., many multicolor maps and black-and-white sketches. £40.—Readers of these review pages are acutely aware that there has been a flood of state, and even county, breeding bird atlases in recent years. More are on the way as "atlasing" has become a popular "sport" for both birders and ornithologists. The atlas concept was introduced to the birding community by the British and Irish ornithologists, who in 1976 published the first "Atlas of Breeding Birds in Britain and Ireland" from field work in the period 1968–1972. The idea spread throughout the world, and the many atlasers and the compilers, who have worked long and hard, can be justifiably proud of their results which have equaled or even surpassed the British effort.

But now comes "The Breeding Bird Atlas: The Next Generation!" "The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991" sets a new mark for the rest of the world to shoot at. It is an outstanding job, both in the field work that went in to it, and the handsome format of publication.

One criticism of the conventional atlas is that the reader gets the idea that a species which occurs throughout the given area is equally abundant throughout. The organizers of this project have made an attempt to solve this problem and have arrived at a method of expressing abundance. Each 10 × 10 km Atlas block was divided into 25 "tetrads" (2 × 2 km small blocks). Observers were instructed to visit at least eight tetrads in a block, and compile a species list after exactly two hours spent in the tetrad. From the fraction of tetrads having the species, an index of abundance was computed. These indices are displayed on a map printed in 10 colors. For seabirds and other colonial species, actual counts were made.

The conventional atlas map recognizes two levels of presence: seen or possible, but no direct breeding evidence, and probable or confirmed breeding evidence. Because of the emphasis on the quantitative work, less effort was expanded on confirming breeding than in the earlier atlas.

A third map in most accounts plots the change in presence from the earlier work. Thus a careful study of this map shows range expansions or contractions since 1972.

Each breeding species is given a two-page spread. Besides the three maps, there is an attractive sketch of the species, often in interesting activity, and about one page of text.

The Atlas concludes with a careful analysis of the changing status of the breeding birds over the period of the two atlases and the intervening years. The number of breeding species increased by three in Britain and by two in Ireland from the earlier results, but the changes were more pronounced than the numbers might indicate. In Britain, four species that bred in 1968–1972 did not breed in 1988–1991, while five species bred in the second period that did not breed in the first. In addition eight species bred in the years 1973–1987 but were not present during the time of both Atlas projects. A total of 89 species had positive distributional changes, while 113 showed negative changes. These are analysed by habitat.

In an attempt to check the tetrad method of determining abundance for bias and error, two additional abundance projects were carried out. After a discussion of general methods of estimating populations, a table of estimated populations of all species is given. These numbers range from several million for such species as House Sparrow (*Passer domesticus*), Blue Tit (*Parus caeruleus*), and Willow Warbler (*Phylloscopus trochilus*) to such low numbers as 1–2 pairs for Brambling (*Fringilla montifringilla*) and 0–1 pair for Red-backed Shrike (*Lanius collurio*).

The New Atlas sets a high standard; it remains to be seen if American atlases of the future can match it.—George A. Hall.

CURRENT ORNITHOLOGY. Vol. 11. Dennis M. Power (ed.). Plenum Press, New York, New York. 1993:292pp—This book, the most recent volume in the series, includes chapters on population trends in the eastern United States, social organization of birds in the nonbreeding season, predation of birds, and effects of life history parameters on length of incubation and hatching asynchrony in altricial birds. The quality of these chapters, as usual, is quite high. The editing is good, resulting in readable prose relatively free of error. The chapters are consistent in format and appearance.

The first chapter, by Robert A. Askins, reviews the decline of North American birds and supports the contention that many species of terrestrial birds have declined over the past 25 years. However, Askins shows that, while populations of many species of forest migrants have decreased at particular sites, most species of forest migrants have shown an overall increase during the past 25 years. Long-term trends are difficult to determine because of wide fluctuations from year to year. Furthermore, grassland and shrubland birds have likewise diminished over the period. Fragmentation of forest and loss of winter habitat in Mexico, Central America, and the Greater Antilles are serious influences on bird abundance.

In the second chapter, William Mm. Block and Leonard A. Brennan review the habitat concept in ornithology and provide a stimulating discussion of the ways in which habitat can be used as a unifying concept.

Erik Matthysen discusses nonbreeding social organization in migratory and resident birds in chapter 3. He reviews populations that maintain associations outside the breeding season and analyzes the benefits of such behavior.

Chapter 4 by I. Newton deals with predation and limitation of bird population densities. He provides a comprehensive review of the possible types of predator–prey interactions that can depress bird breeding numbers below what would otherwise occur. He provides a very insightful look at the effects of predators both by themselves and in the more complex reality of natural ecosystems.

The final chapter by Robert E. Ricklefs is a very extensive review of sibling competition, hatching asynchrony, incubation period, and life span in altricial birds. I found this chapter particularly persuasive and stimulatory. It is meticulous in its logic and focus. Students of clutch size, brood development, and the nesting cycle should read his discussion of theories of hatching synchrony and the evolution of incubation period as possibly affected by just about every conceivable variable.

As in past volumes, this book provides a tremendous service to both new students and more experienced researchers. The discussions provided allow the beginner to quickly come up to speed in specific areas and undoubtedly promote the quality of thesis/dissertation research as a result. For more experienced readers they provide new viewpoints, corrections of misconceptions, and a means of checking what we think we already know. Thank you, Plenum Press, for continuing to publish these valuable reviews.—C. R. Blem.

This issue of *The Wilson Bulletin* was published on 8 March 1995.

The Wilson Bulletin

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CONTENTS

MAJOR PAPERS

A NEW SPECIES OF PYGMY-OWL (STRIGIDAE: *GLAUCIDIUM*) FROM THE EASTERN ANDES ..... *Mark B. Robbins and Steve N. G. Howell* 1

SPECIES LIMITS OF THE LEAST PYGMY-OWL (*GLAUCIDIUM MINUTISSIMUM*) COMPLEX ..... *Steve N. G. Howell and Mark B. Robbins* 7

HABITAT SELECTION IN WOODLAND NEARCTIC–NEOTROPIC MIGRANTS ON THE ISTHMUS OF TEHUANTEPEC I. AUTUMN MIGRATION ..... *Kevin Winker* 26

A COMPARISON OF BIRD COMMUNITIES IN BURNED AND SALVAGE-LOGGED, CLEARCUT, AND FORESTED FLORIDA SAND PINE SCRUB ..... *Cathryn H. Greenberg, Lawrence D. Harris, and Daniel G. Neary* 40

WETLAND USE BY BREEDING AND POSTBREEDING FEMALE MALLARDS IN THE ST. LAWRENCE RIVER VALLEY ..... *Michael P. Losito and Guy A. Baldassarre* 55

SPRING FEEDING ECOLOGY OF CINNAMON TEAL IN ARIZONA ..... *James H. Gammonley* 64

PREDATOR-PREY RELATIONSHIP BETWEEN WILSON'S PLOVERS AND FIDDLER CRABS IN NORTH-EASTERN VENEZUELA ..... *Michel Thibault and Raymond McNeil* 73

LOSSES OF RED-COCKADED WOODPECKER CAVITY TREES TO SOUTHERN PINE BEETLES ..... *Richard N. Conner and D. Craig Rudolph* 81

THE AVIAN CECUM: A REVIEW ..... *Mary H. Clench and John R. Mathias* 93

BIAS IN CHRISTMAS BIRD COUNTS FOR SPECIES THAT VISIT FEEDERS ..... *Erica H. Dunn* 122

NON-MIGRATORY MOVEMENTS OF DUNLINS ON THEIR CALIFORNIA WINTERING GROUNDS ..... *Nils Warnock, Gary W. Page, and Lynne E. Stenzel* 131

INVESTIGATOR DISTURBANCE, CHICK MOVEMENT, AND AGGRESSIVE BEHAVIOR IN RING-BILLED GULLS ..... *Kevin M. Brown and Ralph D. Morris* 140

A TEST OF AN ASSUMPTION OF DELAYED PLUMAGE MATURATION HYPOTHESES USING FEMALE TREE SWALLOWS ..... *George A. Lozano and Paul T. Handford* 153

SHORT COMMUNICATIONS

CAPSAICIN DETECTION IN TRAINED EUROPEAN STARLINGS: THE IMPORTANCE OF OLFACTION AND TRIGEMINAL CHEMORECEPTION ..... *J. Russell Mason and Larry Clark* 165

DEPREDATION OF ARTIFICIAL OVENBIRD NESTS IN A FOREST PATCH ..... *Eric T. Linder and Eric K. Bollinger* 169

DIET OF NESTING KILLDEER IN NORTH DAKOTA ..... *Jeanne M. Fair, Patricia L. Kennedy, and Lowell C. McEwen* 174

UNUSUAL MARBLED MURRELET NEST ..... *Cheri Ford and Mike Brown* 178

THE PARASITIC BLOW FLY, *PROTOCALLIPHORA SPATULATA*, IN TWO NEW HOST SPECIES ..... *Jeanne M. Fair and Clinton K. Miller* 179

FRUIT IN THE DIET OF NESTLINGS OF THE PUERTO RICAN TODY, A TROPICAL INSECTIVORE ..... *Michele Merola* 181

NOTES ON THE NESTING BEHAVIOR OF THE WHITE-BELLIED WOODPECKER ..... *A. Townsend Peterson, Nina Ingle, and Renato Fernandez* 182

ORNITHOLOGICAL LITERATURE 185

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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 107, NO. 2 JUNE 1995 PAGES 193–396

(ISSN 0043-5643)

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

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THE WILSON BULLETIN
(ISSN 0043-5643)

THE WILSON BULLETIN (ISSN 0043-5643) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Second-class postage paid at Lawrence, KS. POSTMASTER: Send address changes to THE WILSON BULLETIN, P.O. Box 1897, Lawrence, KS 66044-8897.

Back issues or single copies are available for $12.00 each. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109.

Subscriptions, changes of address and claims for undelivered copies should be sent to the OSNA, P.O. Box 1897, Lawrence, KS 66044-8897. Phone: (913) 843-1221; FAX: (913) 843-1274.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

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A portrait of a bird, probably a juvenile Field Sparrow, thought to have been painted by William Bartram and loaned to Alexander Wilson when he was learning to sketch birds. Image actual size.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 107, NO. 2 JUNE 1995 PAGES 193–396

Wilson Bull., 107(2), 1995, pp. 193–213

HISTORIC AND TAXONOMIC IMPLICATIONS OF RECENTLY FOUND ARTWORK IN ARITHMETIC BOOKS OF STUDENTS OF ALEXANDER WILSON

EDWARD H. BURTT, JR.[1] AND WILLIAM E. DAVIS, JR.[2]

ABSTRACT.—In 1991, The Gutman Library of Harvard University received four handwritten arithmetic books dating from 1800–1803. Two of the books were decorated with stylized birds and a watercolor drawing of a bird was found in one of the books. We conclude that the drawing is of a juvenile Field Sparrow (*Spizella pusilla*), although other species are possible and are discussed. We further conclude that the artist was probably William Bartram. Notes found in the handwritten arithmetic books attribute the decorations to Alexander Wilson, but the evidence is circumstantial and open to alternative explanations. The decorations are mostly of stylized birds rendered in different colors of ink and completed before Wilson's decision to catalogue the birds of North America and his commitment to learn to paint birds under the guidance of William Bartram, an accomplished illustrator and naturalist. If Wilson's, the decorations indicate that he possessed considerable artistic ability and interest in birds prior to undertaking his remarkable "American Ornithology." *Received 15 Jan. 1993, accepted 2 April 1994.*

In November 1991, we learned that the Gutman Library, Harvard University, had received a set of handwritten arithmetic books belonging to Charles and William Wood who attended the school at Gray's Ferry taught by Alexander Wilson (1766–1813). The books had been decorated with birds and an undated, unsigned drawing of an unknown bird was found in one of the books. Notes added to the arithmetic books by descendents of Charles and William Wood attribute the decorations to Alexander Wilson whose nine volume "American Ornithology" (1808–1814) was the first systematic catalog of the birds of North America. To achieve his masterpiece, Wilson taught himself to sketch and paint birds under the tutelage of William Bartram, the foremost American naturalist of the late

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eighteenth and early nineteenth centuries. In this context, the painting and decorations become important to our understanding of Wilson's artistic ability and development, but did Alexander Wilson paint the bird portrayed in the unsigned watercolor? When was the bird painted? And what species is portrayed? What about the decorations? Were they drawn by Alexander Wilson? Can they tell us anything about Wilson's artistic abilities and interests?

THE ARTIST

The painting (Frontispiece) is unsigned, but was in one of the handwritten arithmetic books from students at the school where Alexander Wilson taught. However, the composition and style are not consistent with Wilson's sketches and published portraits of birds. The Frontispiece contains a bird and a complete, anatomically correct gentian, probably *Gentiana andrewsii* or *G. saponaria* (D. Johnson, pers. comm.). Wilson portrayed 316 birds in his nine volume "American Ornithology," but only the portrait of the male Ruby-throated Hummingbird (*Archilochus colubris*) contains a flower, and that flower includes only a short section of stem and a single cluster of leaves. The flower appears to be a delphinium (*Delphinium* sp., D. Johnson, pers. comm.), but its lack of detail precludes positive identification. The bird in the frontispiece is perched on the blossom of the gentian, but the blossom could not support the bird, nor is the bird grasping the blossom. Wilson's songbirds firmly grasp branches that are capable of supporting them. The inclusion of a flower and a bird that is not grasping its perch are features sufficiently uncharacteristic of Wilson's work as to cast doubt on his being the artist.

If the painting dates from the time of the arithmetic books, which are dated 1800, 1801, 1803, and undated, who other than Wilson was painting birds? At the turn of the nineteenth century William Bartram (1739–1823) was the best known of America's naturalists. He had travelled and lived in the Carolinas, Georgia, and Florida (Harper 1958), and from 1773–1777 he illustrated the plants and animals of the southeast and kept a detailed journal on which he based his "Travels through North and South Carolina, Georgia, East and West Florida" (1791). Following the death of his father, John Bartram, in 1777, William returned to the family home at Gray's Ferry, just outside Philadelphia, where he spent the rest of his life writing, sketching, and caring for the famous botanical garden begun by his father. A few of William Bartram's illustrations can be seen in his "Travels," but most were sent to England to Peter Collinson or Dr. John Fothergill who funded Bartram's exploration of the southeastern United States. Some of these illustrations have been published by Ewan (1968), and many unpublished illustrations are in the archives of the Academy

of Natural Sciences of Philadelphia, American Philosophical Society, and Historical Society of Pennsylvania. Also active at this time was John Abbot (1751–1840), a British immigrant to Georgia and prolific painter of insects and birds for European patrons (Rogers-Price 1983). A collection of Abbot's watercolors of birds is at the Houghton Library, Harvard University. Wilson refers to the artistic pursuits of Ann Bartram Carr (1779–1858), William Bartram's niece and housekeeper, in no less than nine letters from 4 March 1803 to 22 May 1807 (Hunter 1983). We were unable to locate any of her original work but studied a microfilm copy of her only published illustration (Barton 1805). John James Audubon (1785–1851) began painting birds in 1805 (Davidson in Audubon 1966), probably after the portrait had been painted. Nonetheless, we compared the portrait to Audubon's published watercolors (Audubon 1966) on which the plates for his "Birds of America" (1827–1838) are based. Still later were Alexander Rider, who immigrated to America from Germany in 1810, and Titian Peale (1799–1885), illustrators for Bonaparte's "American Ornithology" (1825–1833). A selection of their work is at the Academy of Natural Sciences of Philadelphia. These artists and their works, along with Wilson's "American Ornithology" (1824) in the rare book collection at Beeghly Library, Ohio Wesleyan University, and his sketches and letters at the Houghton Library, Harvard University, Museum of Comparative Zoology (MCZ) Library, Harvard University, and the Academy of Natural Sciences of Philadelphia, form the basis for our analysis of the portrait.

The presence of an anatomically correct gentian (Frontispiece) suggests that Bartram, who was a knowledgeable botanist and whose bird portraits usually include one or more plants, was the artist. Furthermore, the gentian grows from ground strewn with miniature mushrooms, rocks, and grasses. Such miniaturized objects are a common feature in the foregrounds of Bartram's illustrations. The bunch of bent and twisted grass in the lower left (Frontispiece) resembles bunches of grass found in many of Bartram's foregrounds. Abbot, like Bartram, employed miniaturized foregrounds, and he occasionally included flowers and grasses, but his flowers are not anatomically correct, and his grasses are neither bent nor twisted. Carr's Brown Creeper (*Certhia americana*) is too large for its tree, but miniaturized plants and objects are absent. Wilson included foregrounds in only 42 of the 76 plates in "American Ornithology," but miniature objects are entirely lacking. Occasionally, Wilson included a bunch of grass, but it is not bent and twisted as in the portrait and in Bartram's illustrations. Audubon, Rider, and Peale provide only naturalistic settings that are in proportion to their birds.

The twisting of the bird's head is unusual, but the same posture occurs

in nine of 16 (56%) bird illustrations by William Bartram (Ewan 1968). Abbot used the posture in 15 of 61 (25%) illustrations, but Wilson used a similar posture in only 24 of his 316 portraits (8%). Among the later natural history illustrators, only Rider used the posture (7 of 46 illustrations [15%]).

The anatomy and proportions of the bird are characteristic of Bartram's bird illustrations. For example, the bird's eye is too close to the bill (Frontispiece), a universal feature of Bartram's birds. Wilson placed the eye farther back in its correct position, as did John Abbot, Ann Bartram Carr, and other artists of the period. The prominent, semi-circular plumage pattern of the auricular area (Frontispiece) occurs on most of Bartram's birds, on the creeper of Carr, but not on the birds of Abbot, Wilson, Rider, Peale, or Audubon. The pointed scapular feathers that overlap the wing (Frontispiece), are found only on the bird portraits of Bartram and Carr. The primary coverts of the portrait are aligned with the primaries (Frontispiece). Such alignment occurs in the portraits by Bartram, Carr, and Abbot, but Wilson and later illustrators curve the primary coverts, which is correct. The hallux on the raised foot of the portrait is extended back, but when a bird lifts its leg the hallux relaxes toward the other toes not backward. Occasionally Wilson and Audubon portrayed a bird with its foot raised, and in every portrayal the hallux hangs forward. More importantly the legs of the bird in the Frontispiece lack detail. They are outlined and the scales indicated by a few cross lines. Such approximation is characteristic of Bartram, Abbot, and Carr, but not Wilson whose draftsmanship is described by Charles Robert Leslie (Cantwell 1961), one of Wilson's early colorists and later court painter to Queen Victoria:

> "We worked from birds which he had shot and stuffed, and I remember the extreme accuracy of his drawings, and how carefully he had counted the number of scales on the tiny legs and feet of his subject."

The portrait's tail is twisted to give us a dorsal view. Such a view can be found in several of Bartram's sketches. A less extreme twist occurs in some of Abbot's bird portraits and in Carr's creeper, in only a few of Wilson's early illustrations, and in none of the portraits by Rider, Teale, or Audubon. In composition, style, anatomy, and proportion, the portrait (Frontispiece) is consistent with the known work of William Bartram, less consistent with the single known work of Ann Bartram Carr, and inconsistent with the known works of Alexander Wilson, John Abbot, Alexander Rider, Titian Peale, and John James Audubon. However, the watercolor might be Wilson's early rendering of a portrait by Bartram.

Alexander Wilson met William Bartram sometime in 1802 (Hunter

1983), soon after he became master of the school at Gray's Ferry. Wilson's interest in drawing and birds is first expressed in an undated letter, believed to be from 1803 (Hunter 1983) in which he requests advice from Bartram on several "rough draughts" of birds. Later in a letter dated 17 November 1803 Wilson writes:

> "I have taken the liberty of sending you another Specimen of attempts to imitate your beautiful Engravings, presuming on your goodness."

Could the newly found watercolor represent the only surviving copy of a Bartram engraving sketched by Alexander Wilson during the period when he was learning to draw and paint birds under Bartram's tutelage? The gentian lacks detail (Frontispiece), which is uncharacteristic of Bartram whose plants are detailed, even in his illustrations of birds. However, by mid-1803 Wilson had decided to illustrate all of America's birds (Hunter 1983), and if Wilson was copying Bartram's drawing, the greater detail of the bird relative to the gentian might reflect Wilson's interest in understanding avian anatomy and proportion.

Two lines of evidence weigh strongly against this exciting possibility. Close examination of the original suggests that the painting was done entirely in watercolor. Along their length the lines vary slightly in width and intensity of color, as if done by a brush with more or less pressure applied. A collection of his works at the American Philosophical Society shows that Bartram occasionally sketched entirely in watercolor, whereas examination of more than 100 of Wilson's bird portraits housed at the MCZ at Harvard indicates that Wilson outlined his bird subjects in pencil and then rendered them with pen-and-ink, often adding watercolor secondarily. Furthermore, Wilson's earliest drawings for his "American Ornithology" were strictly pencil or pen-and-ink sketches. The coloring was done only after the engraving was completed. Not until later volumes did Wilson supply fully colored drawings to his engraver (Christy 1926). This suggests that Wilson's use of watercolor, such as seen in the portrait, came later, not earlier, in his artistic development, but Wilson's later portraits are better proportioned and more anatomically detailed than his earlier portraits and the bird in the Frontispiece.

The second line of evidence comes from the paper used in the portrait. When light shines through the paper a coarse grid of vertical and horizontal lines is evident along with an incomplete watermark. The grid indicates that the portrait is painted on "laid" paper, a type of paper made and used widely until the very early 1800s (Hunter 1952). "Wove" paper, which replaced "laid" paper, lacks the grid. It was developed in England in the mid-1700s and introduced to the United States in 1795. Because

of its more uniform surface, "wove" paper was preferred by printers and calligraphers, and by 1815 "wove" paper predominated (Hunter 1952). The archives of the American Philosophical Society have 57 drawings by Bartram, of which 34 (60%) are on "laid" paper and 23 on "wove" paper. By contrast all of Wilson's 120 drawings housed in the MCZ at Harvard are on "wove" paper, although Wilson occasionally used "laid" paper for his letters as late as 2 October 1807 (letter to Samuel Bradford concerning subscriptions to "American Ornithology").

The watermark is an incomplete shield surrounding the base of a fleur-de-lis. Below the shield is a 4, and below that three initials, a very clear VG, and the top of what might be an L to the left of the V. The only match is the watermark of Lubertus Van Gerrevink, a famous Dutch papermaker of the 18th century who owned mills throughout western Europe (Gravell and Miller 1983). We can find no record of the watermark after the 1790s. Among Bartram's sketches at the American Philosophical Society are four on "laid" paper with the watermark of Lubertus Van Gerrevink exactly as found in the portrait.

Because Wilson's technique differs from that used in the portrait and because the portrait is on "laid" paper, whereas Wilson used only "wove" paper for his bird portraits, we conclude that the painting is neither an early sketch by Alexander Wilson nor Wilson's copy of Bartram's work. Based on the presence of an anatomically correct gentian, the miniaturized foreground with its bent and twisted bunch of grass, the anatomy and proportions of the bird, the exclusive use of watercolor on "laid" paper of late 18th century Dutch origin, paper known to be used by William Bartram, we conclude that the portrait artist was indeed William Bartram.

SPECIES IDENTIFICATION OF THE PORTRAIT

William Bartram, and the naturalist-illustrators of the late 18th and early 19th centuries based their paintings of birds on specimens, which means the bird in the painting is based on a real bird collected from the wild. Bartram spent his long life in southeastern Pennsylvania, except for his travels and natural history studies in the southeastern United States from 1773–1777. Therefore, the species portrayed probably comes from southeastern Pennsylvania or possibly the southeastern states.

The heavy bill suggests that the bird is a bunting (Emberizidae, Cardinalinae) or sparrow (Emberizidae, Emberizinae), but the coloration and pattern of color do not match that of any eastern species. We have compared the portrait to specimens of eastern North American emberizines and have shown colored photocopies to colleagues for their identification of the portrait. Several species and one hybrid have been suggested as

possibilities (Table 1). We have examined specimens of these species at the Carnegie Museum of Natural History, Harvard Museum of Comparative Zoology, and the University of Michigan Museum of Zoology. We compared the colors and patterns of the possible species to the painting and then compared physical measurements and proportions. We consider the species in taxonomic sequence.

The general brownish color and lack of distinctive field marks suggests a female Indigo Bunting (*Passerina cyanea*), but the Indigo Bunting lacks the faint eye-ring and wing bars seen in the portrait (Frontispiece, Table 1). Furthermore, the female bunting's brown dorsum is not finely streaked as in the unidentified portrait (Frontispiece, Table 1) nor is the dorsum as dark as in the portrait nor the dorsal-ventral contrast as great (Frontispiece). Furthermore, female buntings have blue edges to the primaries and rectrices (Table 1), a feature not found in the portrait. Because of its similar coloration the female Indigo Bunting cannot be completely ruled out as the subject of the portrait, but the many differences in detail make it an unlikely subject.

The dark face, gray-brown back, and light venter suggest a juvenile Rufous-sided Towhee (*Pipilo erythrophthalmus*). However, the towhee differs in many details. For example, the towhee has no eye-ring, its wing-bars are more prominent than those of the portrait, its outer tail feathers have large patches of white, and its legs and bill are brown, not pink (Table 1). The dominant ground color of the portrait is brown, whereas that of the juvenile towhee is cinnamon (Frontispiece, Table 1). The dissimilarities of color and pattern (Table 1) far outnumber the similarities and suggest that a juvenile towhee is not the subject of the painting.

The pink bill and legs combined with the faint wing-bars and indistinct markings of the breast suggest a juvenile Field Sparrow (*Spizella pusilla*). Furthermore, details of color and pattern tend to agree (Table 1). The portrait and the juvenile Field Sparrow have faint eye-rings and areas of brown that are finely streaked with darker brown. These fine streaks are formed when the vane near the rachis is darker than the outer edge of the vane. The artist illustrates this with fine dark brush strokes as can be seen on the back of the bird in the painting. The bird is perched with its side to the viewer with its head turned away so that it can look at the viewer with its right eye over its left shoulder. We suggest that the gray between the breast and the head is the color of the upper back and nape where the neck twists around. The white throat visible below the bill indicates that the pinkish buff breast leads to a white throat and is not crossed by gray. The pattern of light belly, slightly darker breast, light throat, and darker neck and nape is the pattern of a juvenile Field Sparrow (Table 1). The juvenile Field Sparrows we examined had fine streaks on

TABLE 1

COMPARISON OF COLOR AND PATTERN BY TOPOGRAPHIC SURFACE OF THE UNIDENTIFIED PORTRAIT AND ITS POSSIBLE SPECIES

Topography	Portrait	Indigo Bunting (female)	Rufous-sided Towhee (juvenile)	Field Sparrow (juvenile)	Lincoln's Sparrow (juvenile)	White-throated Sparrow (juvenile)	White-throat × Junco (adult, male)	Dark-eyed Junco (juvenile)
Crown	Reddish brown	Brown	Cinnamon, dk. brown streaks	Brown	Chestnut, small black streaks	Dk. brown, light central stripe	Dark gray-brown	Gray-brown, dk. brown streaks
Forehead	Dark brown	Brown	Cinnamon, dk. brown streaks	Brown	Chestnut, small black streaks	Dk. brown, light central stripe	Dark gray-brown	Gray-brown, dk. brown streaks
Eyebrow	Reddish brown	Brown	Dark brown, light flecks	Brown	Gray	Lt. brown, yellow near bill	Dark gray, bit of white near bill	Gray-brown, dk. brown streaks
Eye line	Brown	Brown	Dk. brown	Brown	Dk. brown	Gray	Dk gray	Gray-brown, dk. brown streaks
Eye-ring	Lt. brown, faint line	Brown	Dk. brown	Lt. brown, faint line	Lt. brown, faint line	Gray	Dk gray	Gray-brown, dk. brown streaks
Auricular	Gray brown	Brown	Dk. brown	Brown	Gray	Gray	Dk gray	Gray-brown, dk. brown streaks
Nape	Dk. brown	Brown	Dk. cinnamon, dk. brown streaks	Brown	Gray-brown, dk. brown streaks	Dk. brown, lt. central stripe	Dk. brown, gray	Gray-brown, dk. brown streaks

TABLE 1
CONTINUED

Topography	Portrait	Indigo Bunting (female)	Rufous-sided Towhee (juvenile)	Field Sparrow (juvenile)	Lincoln's Sparrow (juvenile)	White-throated Sparrow (juvenile)	White-throat × Junco (adult, male)	Dark-eyed Junco (juvenile)
Back	Brown, small, dk. brown streaks	Brown	Dk. cinnamon, dk. brown streaks	Brown, dk. brown streaks	Gray-brown, dk. brown streaks	Brown, dk. brown streaks	Brown, dk. brown streaks	Gray-brown, dk. brown streaks
Scapulars	Brown, dk. streaks, light edges	Brown	Dk. cinnamon, dk. brown streaks	Dk. brown with light edges	Gray-brown, dk. brown streaks	Dk. brown with light edges	Dk. gray	Gray-brown
Rump	Gray-brown	Brown	Dk. cinnamon, dk. brown streaks	Gray-brown	Gray-brown, dk. brown streaks	Cinnamon	Gray-brown	Gray
Uppertail coverts	Gray-brown	Brown	Dk. cinnamon, dk. brown streaks	Gray-brown	Gray-brown, dk. brown streaks	Cinnamon	Gray-brown	Gray-brown, narrow dk. brown streaks
Tail	Dk. gray-brown	Blue-brown	Black, white outer corners	Dk. brown	Dk. brown	Dk. cinnamon	Dk. brown, white outer feathers	Dk. brown-black, white outer feathers
Mustache	Lt. line, gray line below	Gray	Cream	Gray, no contrast	Dk. brown, buff, dk. brown	Dk. brown, white above	Dk. gray	Gray-brown, small dk. brown streaks
Throat	White	White	White, brown spots	White to gray, varies	White	White	White	Lt. gray, dk. edges

TABLE 1
CONTINUED

Topography	Portrait	Indigo Bunting (female)	Rufous-sided Towhee (juvenile)	Field Sparrow (juvenile)	Lincoln's Sparrow (juvenile)	White-throated Sparrow (juvenile)	White-throat × Junco (adult, male)	Dark-eyed Junco (juvenile)
Breast	Pinkish brown, fine streaks	Buff, gray-brown streaks	White, brown streaks	Brown wash, fine streaks	Buff, fine dk. brown streaks	Gray, fine dk. edges on feathers	Dk. gray	Gray, dk. brown streaks
Shoulder	Brown, dk. streaks, lt. feather edges	Brown	Dk. brown	Brown, darker streaks	Gray, dk. brown streaks	Gray	Dk. gray	Gray
Wing bars	Two, lt. edges of coverts	None, brown	Two, buff to white	Two, lt. brown	Two, faint, buff feather edges	Two, buff	Two, white feather tips	None, dk. brown
Flank	White	Buff	Gray-buff, dark streaks	Lt. brown, dk. brown streaks	Buff, dk. brown streaks	Lt. brown	Gray	Gray
Belly	White	White	White	White	White	White	White	White
Primaries	Dk. brown	Dk. brown, blue edges	Dark brown, edged in white	Dk. brown	Dk. brown	Dk. brown, cinnamon edges	Dk. brown	Dk. brown-black
Undertail coverts	White	White	Lt. brown	White	Pale buff	White	White	White
Tarsi	Pink	Black	Brown	Pink	Lt. Brown	Lt. brown	Lt. brown	Pink
Bill	Pink	Black	Dk. brown	Pink	Dk. brown	Lt. brown	Lt. brown	Lt. brown

the breast and flanks (Table 1), which are not seen in the portrait. However, Sutton (1935) describes the juvenal plumage as having spots or flecks on the under parts, a description that closely fits the pattern seen in the portrait. Alternatively, the fine marks on the breast of the bird in the portrait may be the artist's way of indicating the edges of feathers rather than an indication of streaking. General and detailed similarities of color and pattern (Table 1) make the juvenile Field Sparrow a likely subject of the portrait.

The buff tint to the upper breast, gray on the neck, and the faint wingbars suggest a juvenile Lincoln's Sparrow (*Melospiza lincolnii*). Like the Field Sparrow, the similarities extend to details of color and pattern (Table 1); for example, the faint eye-ring and the white belly, buff breast with fine, dark streaks, and white throat. However, the streaked forehead of the juvenile Lincoln's Sparrow is absent in both the juvenile Field Sparrow and the portrait, and the streaking of the breast and flanks is more pronounced in the juvenile Lincoln's Sparrow than in the juvenile Field Sparrow or the portrait. Furthermore, the tarsi and bill of the juvenile Lincoln's Sparrow are brown, not pink as in the Field Sparrow (Table 1) and the portrait. Nonetheless, the juvenile Lincoln's Sparrow is a possible subject of the portrait.

The white throat and gray upper breast suggest a juvenile White-throated Sparrow (*Zonotrichia albicollis*). This identification assumes that the gray across the upper breast represents the upper breast and not the sides of the neck as it twists toward the turned head. The white throat bordered by a gray line which is bordered in turn by a light line strongly suggests the throat pattern of a juvenile White-throated Sparrow, but the head stripes, the cinnamon color of the lower back, the gray face, and the brown bill and legs that characterize the White-throated Sparrow (Table 1) are not characteristics of the portrait. Like the towhee, the White-throated Sparrow is an unlikely model for the bird in the portrait.

Unlike the White-throated Sparrow, the portrait lacks head stripes. However, hybrid White-throated Sparrow × Dark-eyed Juncos have gray-brown plumage in place of the sparrow's prominent head stripes (Table 1), but retain the white throat (Townsend 1883, Stone 1893) also present in the portrait. In addition, the gray-brown rump and upper tail coverts of the hybrid match the painting better than does the cinnamon color of the White-throated Sparrow. The upper breast of the hybrid is gray (Table 1), which may be the color of the upper breast in the portrait, but alternatively the gray across the upper breast of the portrait may represent the sides and back of the neck where the head is turned away from us. The hybrid lacks the faint eye-ring and pink bill and legs of the portrait, and is too gray overall (Table 1). Most importantly, the hybrid has white outer

tail feathers not seen in the portrait. Taken together the similarities make the hybrid a more likely subject than the White-throated Sparrow, but the dissimilarities make it less likely than the Indigo Bunting, Field Sparrow, and Lincoln's Sparrow.

The dark face, gray-brown back, and light venter suggest a juvenile Dark-eyed Junco (*Junco hyemalis*). However, like the hybrid, the general similarity of the junco and the portrait cannot withstand detailed comparison. The head of the portrait lacks the junco's fine streaks and has an eye-ring which the junco lacks (Table 1). The junco also lacks the white throat and wing bars of the portrait (Table 1), and the portrait lacks the white outer tail feathers of the junco. Although the legs of both are pink (Frontispiece, Table 1), the junco's bill is light brown (Table 1) whereas the bill in the portrait is pink. The Dark-eyed Junco bears a general resemblance to the portrait, but many differences in detail make it an unlikely model for the portrait.

In addition to color and pattern, the size and proportions of the portrait may indicate its identity. Most of Bartram's illustrations are life-size (Porter 1989, pers. obs.), and Wilson's songbirds are life-size and properly proportioned (Leslie as cited in Cantwell 1961). The total length of the bird in the painting cannot be measured accurately because of its turned head, but the lengths of the wing, tail, tarsus, and culmen were measured with steel calipers. The wings of specimens were measured by slipping a steel ruler under the wing and reading the chord length. The wing on the portrait was measured from the intersection of the leading edge and the overlying scapular feathers to the wing tip. The tail was measured from where the outermost tail feather emerged from the uppertail coverts to its tip. This was the greatest length of the tail in the painting and minimized error. The tarsus was measured from the base of the middle toe on the left foot to the outer bend of the left leg. The culmen was measured from the base of the right nostril to the tip of the bill (Table 2).

The juvenile Lincoln's Sparrow most closely matches the portrait for wing length, although the juvenile Field Sparrow and female Indigo Bunting are also very close. The tail length of the portrait is most similar to that of the female Indigo Bunting and only slightly less similar to the tail length of the juvenile Lincoln's Sparrow. The other species have considerably longer tails. The portrait has a shorter tarsus than any of the specimens, but the female Indigo Bunting and juvenile Field Sparrow have the most similar tarsal length, with the juvenile Lincoln's Sparrow being only slightly longer. The culmen length is short and differences slight, but the portrait and the juvenile Field Sparrow have the same length, while the female Indigo Bunting, juvenile Lincoln's Sparrow, and juvenile Dark-eyed Junco are only 0.5 mm longer. To estimate overall agreement

TABLE 2

COMPARISON OF MEASUREMENTS (MM) AND (IN PARENTHESES) PROPORTIONS BASED ON THE RATIO OF THE LENGTH OF THE WING CHORD, TAIL, OR BILL TO THE LENGTH OF THE TARSUS FOR THE UNIDENTIFIED PORTRAIT AND ITS POSSIBLE SPECIES OR HYBRID

Measurements (mm)	Portrait	Indigo Bunting (female)	Rufous-sided Towhee (juvenile)	Field Sparrow (juvenile)	Lincoln's Sparrow (juvenile)	White-throated Sparrow (juvenile)	White-throat × junco (adult, male)	Dark-eyed Junco (juvenile)
Wing chord length	59	64.5	89	63	60	72.5	76.5	77
	(4.21)	(4.03)	(3.07)	(3.94)	(3.53)	(3.29)	(3.64)	(4.05)
Tail	43	41	87	55	48	66	61	59
	(3.07)	(2.56)	(3.00)	(3.44)	(2.82)	(3.00)	(2.90)	(3.10)
Tarsus	14	16	29	16	17	22	21	19
Culmen	6.5	7	10.5	6.5	7	9	8	7
	(0.46)	(0.44)	(0.36)	(0.41)	(0.41)	(0.41)	(0.38)	(0.37)
Total deviation from measurements of portrait[a]		10	93	18	9.5	37	44	39.5

[a] The total deviation is calculated by taking the absolute value of the difference between the wing, tail, tarsus, or culmen length of the species or hybrid and the same measurements of the portrait, then summing all values for the column.

of measurements, we took the absolute value of the difference in the length of the wing, tail, tarsus, and culmen between the portrait and each species or hybrid. We then summed the differences for that species or hybrid to provide a quantitative estimate of the match. The juvenile Lincoln's Sparrow is the best overall match to the portrait, but the female Indigo Bunting matches almost as well (Table 2). The juvenile Field Sparrow was an excellent match to the portrait except for its tail, which was much longer than that of the bird in the painting (Table 2). The juvenile White-throated Sparrow, juvenile Dark-eyed Junco, and hybrid are all larger than the bird in the painting (Table 2), particularly in the wings and tail. The juvenile towhee is much too large (Table 2).

The portrait is smaller than all possible species and the hybrid, but its proportions might match closely one of the suggested identifications. To test this possibility, we took the tarsus as our standard and calculated the other measurements as a ratio of tarsal length (Table 2). The proportions of the juvenile Dark-eyed Junco are the most similar to those of the portrait with the proportions of the juvenile Field Sparrow and the female Indigo Bunting being only slightly less similar (Table 2). The proportions of the juvenile Rufous-sided Towhee, juvenile White-throated Sparrow, and hybrid are the least well matched to the portrait (Table 2).

On the basis of color and pattern, overall size, and proportions, the juvenile Field Sparrow, juvenile Lincoln's Sparrow, juvenile Dark-eyed Junco, and female Indigo Bunting match the portrait most closely. The juvenile Rufous-sided Towhee, juvenile White-throated Sparrow, and hybrid White-throated Sparrow × Dark-eyed Junco are relatively poor matches. If the portrait was painted by William Bartram, the bird probably was collected in southeastern Pennsylvania, where he lived and observed birds, or in the southeastern states where he had travelled and studied extensively. Dark-eyed Juncos and Lincoln's Sparrows winter in these areas, but they breed farther north and west. In Lincoln's Sparrow the juvenal plumage is replaced by the first winter plumage during a partial molt that is completed by early August (Dwight 1900), well before early September when the first Lincoln's Sparrows arrive in Pennsylvania (Wood 1958). The Dark-eyed Junco acquires its first winter plumage during a partial molt that occurs in August and early September (Dwight 1900), whereas the first juncos arrive in southeastern Pennsylvania in mid- to late September (Eaton 1968). Based on the breeding range, the timing of molt, and the arrival of fall migrants in southeastern Pennsylvania, Bartram would have been unlikely to encounter juvenile Lincoln's Sparrows or Dark-eyed Juncos.

We conclude that the portrait is that of a juvenile Field Sparrow, a common breeding species in southeastern Pennsylvania. We base our conclusion on the similar size and proportions and the close match in color and pattern of the juvenile Field Sparrow and the portrait and on the Field Sparrow's status as a common breeding species in southeastern Pennsylvania.

We suggest that the portrait was loaned or given to Alexander Wilson to copy. We know from Wilson's correspondence with Bartram that this was a common learning technique early in Wilson's artistic development. However, the importance of the painting transcends its value as a teaching tool and confirmation of a teaching method alluded to in Wilson's letters to Bartram. Alexander Wilson is credited with having discovered and described the Field Sparrow (AOU 1983); however, he attributes its discovery to William Bartram (Brewer 1854, p. 174). On page 291 of his "Travels" (Harper 1958), Bartram lists the "Little Field Sparrow" (*Passer agrestis*) among the "Granivorous Tribes" and indicates that it is a summer resident in Pennsylvania, but otherwise does not describe the species or its biology. The type specimen pictured in Wilson's "American Ornithology" (1808–1814), plate 24, is at the Harvard Museum of Comparative Zoology, but if the painting is a juvenile Field Sparrow, it represents an earlier specimen of a Field Sparrow collected and portrayed by William Bartram exactly as stated by Alexander Wilson. The portrait

(Frontispiece) is the iconotype of Bartram's (*Passer agrestis*) and, by Wilson's own attribution, the iconotype of the Field Sparrow (*Spizella pusilla* [Wilson]).

CALLIGRAPHY

In a letter from G. J. O'Connell, executor of the will of Dorothy M. Smith, to M. Canavan, Harvard University, written 13 July 1990 the University was notified that it would receive "all handwritten arithmetic books (circa 1800) of Charles Wood and William Wood, one of the books having been illustrated by Alexander Wilson while he was the teacher of Charles and William." Ann T. Tarr accepted "three handwritten arithmetic books (circa 1800) of Charles Wood and William Wood . . ." in Common Pleas Court in Philadelphia County on 26 June 1991. That is the description of the books in the legal documents pertaining to the gift. In fact, four handwritten, arithmetic books were included in the bequest and two of these are illustrated.

Two of the books bear the name of Charles Wood. One of these contains decorated, calligraphic headings, and its cover is dated 9 Sept. 1800. The other contains block-letter, undecorated headings and its cover is dated 10 Mar. 1803, but a page part way through the book is dated 19 Feb. 1802. The cover dates appear to be the dates on which the books were completed (R. Mathiesen, pers. comm.). The handwriting is the same in both books, presumably the handwriting of Charles Wood. The decorated calligraphy in the 1800 book is markedly different from the block-letter headings of the 1803 book, but very similar to the decorated calligraphy in the arithmetic book of William Wood, which is dated 3 Jan. 1801. The handwriting in this book differs from that in the two books by Charles Wood, thereby confirming that this book was indeed written by a different student. The similarity of the calligraphy and particularly the decorations in lesson books written by different students with different handwriting suggests that the teacher or an assistant was the calligrapher. Two notes in the decorated book of Charles Wood state that Alexander Wilson was that teacher and calligrapher. The larger note states:

> "School Book of Charles Wood—dated 9th Sept. 1800
>
> "Alexander Wilson, the Scottish ornithologist, was school master of the school at Darby Rd. and Greenway Lane, near Sorrel Horse Tavern, at this period.
>
> "The school book, prepared and decorated by the schoolmaster, became the property of Charles Wood, then about 12 years old, who attended this school.

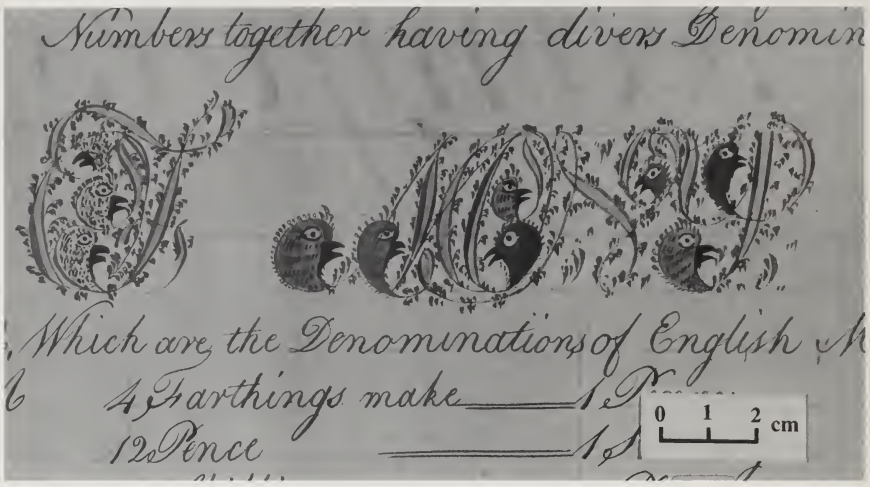

FIG. 1. "Of Money" is an exquisite example of linked lettering in blue and yellow with red and brown flourishes. The ten birds are in blue, yellow, and red outlined in black with red and brown interior detail.

"Charles Wood married Mary Walters, a quakeress at Old Swede's in 1811"

This note is hand-printed in black ink on white card stock, appears to be relatively recent, and was probably used to label the book for a display. The second label is much smaller, is yellowed from age, and the back has patches of dried glue and paper where the label was glued to some surface and later removed. This label states: "This book decorated by Wilson Ornithologist."

The will and the labels attribute the decorations to Alexander Wilson, but these were written long after the decorations were drawn. However, the design of the decorations (Fig. 1) also supports the conclusion that Wilson was the calligrapher. The letters contain many curls from which sprout tiny, colored leaves. Among the curls and leaves are birds with multicolored bodies shaped like inverted tear drops (Fig. 1). The design resembles a traditional paisley print, a pattern that would have come easily to Alexander Wilson who was born in Paisley, Scotland, and worked as an apprentice, and later journeyman weaver from 1779–1794 (Hunter 1983).

The calligraphy also shows a strong German influence (Fig. 2, R. Mathiesen, A. Aninger, pers. comm.), which is not surprising, considering the strong Pennsylvania Dutch (German) presence in the Philadelphia area. Wilson lived with a Pennsylvania Dutch family during his years at

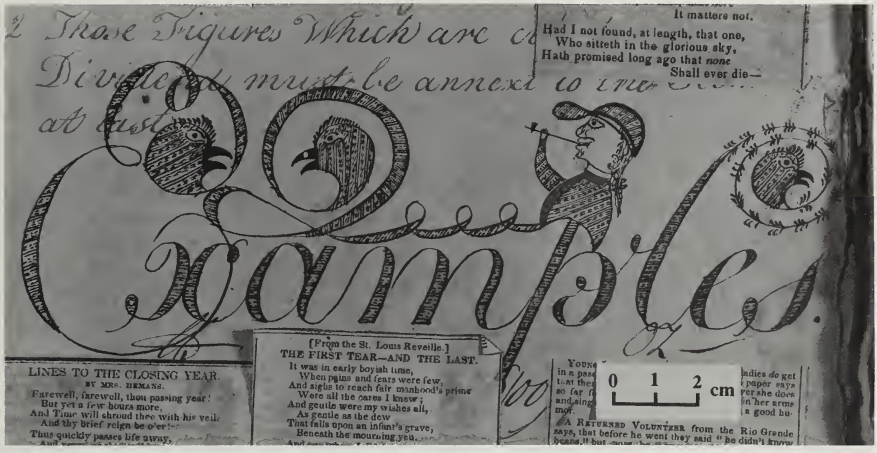

FIG. 2. The man's Hessian pigtail and clay pipe reflect the Pennsylvania Dutch influence. Note the patterned detail of the letters and the four figures, also the leaf-like marks on the flourish encircling the rightmost bird. The "E" overlaps two lines of writing above the heading. The "P" and "L" overlap the line of writing below the heading. Newspaper clippings were glued into the book at a later date.

Milestown (Cantwell 1961), and his letters indicate that he had learned to read, write, and speak German during this period. He also taught penmanship, so that calligraphy was certainly known to him.

The decorated calligraphy of the arithmetic books (Figs. 1 and 3) is unique. It is not typical *fraktur,* the term generally applied to the decorative style developed by the Pennsylvania Germans during the latter part of the eighteenth and first half of the nineteenth centuries. Examination of over 900 photographs of fraktur, by over 300 artists, in the files of the Winterthur Museum, Wilmington, Delaware, and nearly 300 pieces from the Free Library of Philadelphia (Weiser 1976) produced nothing similar to the calligraphy of the arithmetic books. Of 275 fraktur photographs, 85 contain birds, but all are whole birds, none are bird heads, and none of the birds are based on the tear drop motif. Thus, the calligraphy of the arithmetic books, although strongly Germanic, is neither true fraktur nor traditional Pennsylvania Dutch. Its unique decorations suggest the abstract, curved shapes of the palmette motif in Paisley fabrics. The will and the labels point to Alexander Wilson as the artist and Wilson brought both the Germanic and Paisley influences to his position at Gray's Ferry school.

The problem with attributing the calligraphy to Alexander Wilson is that he became schoolmaster of the Gray's Ferry school attended by

FIG. 3. "Of Add(ition)" combines linked lettering decorated with birds, interior detail, large and small flourishes, and black, broken lettering.

Charles and William Wood on 1 March 1802, and all the calligraphy decorated with birds appears to precede that date. We believe that William and Charles Wood did attend the Gray's Ferry school, since a William Wood, presumably the father of William and Charles, is listed on the tax roles of the township from 1780 to after 1800 (J. T. Fry, pers. comm.). Hence there is little chance that the Wood brothers attended the Milestown school where Wilson taught from 1796 to 1801 (Cantwell 1961, Hunter 1983).

Could Wilson have done the calligraphy at a later date? All the calligraphy was done after the lesson on the page had been completed. In all cases where the calligraphy contacts the writing above or below it, the calligraphy is uppermost (Fig. 2), and, thus, was written after the lesson. It was common practice for a schoolmaster or his assistant to reward excellent work by adding decorations. Thus the calligraphy may have been added the same day as the lesson was completed, or shortly thereafter (R. Mathiesen, pers. comm.). However, Wilson could have added the calligraphy at a much later date, after he became schoolmaster at Gray's Ferry school where the Wood brothers wrote their arithmetic books.

One damning piece of evidence makes this unlikely. One decoration is dated "13th Oct. 1800" (Fig. 4), and this is more than sixteen months before Wilson became schoolmaster. Possibly this calligraphy, which is

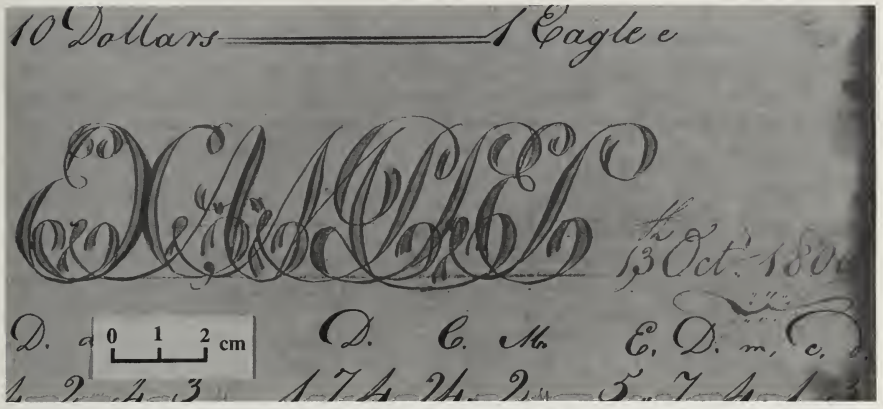

FIG. 4. "Examples 13th Oct. 1800." Though unadorned "Examples" shows the skillful control of line width and curvature that characterizes all the calligraphy. The interlocking letters and the flourishes are characteristic of fraktur, but are skillfully done. By contrast the date is relatively sloppy. The lines have uneven transitions of width, the "o" is not round and the zeros are not oval.

not decorated with birds, was done by someone else and Wilson later penned the bird-decorated calligraphy. We find this unlikely since all the calligraphy appears to be in the same hand. Another possibility is that the calligraphy and the date were written by different persons at different times. Whereas "Examples" (Fig. 4), though undecorated, is skillfully done, the date is less so. As the lines of the date turn around the letters and numbers the width changes unevenly. The capital "O" is not round, and its flourish crosses the top of the letter. The zeros are not oval. These differences in quality could indicate that a student dated the lesson and a teacher decorated it at a later time. We conclude that the decorated calligraphy of the arithmetic books attributed to Alexander Wilson by notes and in the bequest may not have been done by him. However, if the calligraphy and decorations were done by Alexander Wilson, they indicate a strong interest in birds prior to his association with William Bartram and prior to his conceiving the "American Ornithology." Furthermore, the decorations indicate a very considerable artistic talent, which would help account for Wilson's phenomenal development as an artist. Prior to 1803, he had no artistic training. From 1803 until his death in 1813, Wilson's only teacher and critic was William Bartram, yet he produced 316 portraits of birds, some of which are outstanding (Abbott 1943). However, the authorship of the bird-decorated calligraphy remains a fascinating enigma.

ACKNOWLEDGMENTS

We thank John W. Collins, III for bringing the painting and arithmetic books to our attention and for making the materials available to us on several occasions. David Johnson identified flowers. We thank Mary Russell of the Gutman Library of Harvard, Eva Jonas and Dana Fisher of the library at the Museum of Comparative Zoology, Harvard University, Carol Spawn and Daren Stevens of the Academy of Natural Sciences of Philadelphia, and Elizabeth A. Carroll-Horrocks of the American Philosophical Society for assisting us in our study of the original letters and artwork of William Bartram and Alexander Wilson. Joel T. Fry, historian at Bartram's Gardens, answered our questions on dates and relationships within the Bartram family, the location of the schools at Milestown and Gray's Ferry and the location of the Wood family residence. Joseph Ewan, Marion Jenkinson, Robert M. Peck, and John S. Tomer shared their knowledge of early bird paintings with us. Ann Aninger of the Houghton Library, Harvard University and Robert Mathiesen of Brown University helped with our analysis of the calligraphy. E. McSherry Fowble and Bert Denker of the Winterthur Museum, Wilmington, Delaware, were helpful in examining examples of Pennsylvania German fraktur, as was Cornelia King at the Free Library of Philadelphia. Frederick S. Weiser examined photographs of the copy book calligraphy and shared his expertise on fraktur. We thank Raymond A. Paynter, Jr. for providing access to Wilson's specimens. Robert M. Peck coordinated our visits to Philadelphia and offered advice that was vital to understanding the significance of the painting and calligraphy. The manuscript profited greatly from the comments of Richard Connor, John S. Tomer, Robert M. Peck, and an anonymous referee and from the editing of C. R. Blem.

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PHYLOGENY AND COMPARATIVE ECOLOGY OF STIFF-TAILED DUCKS (ANATIDAE: OXYURINI)

Bradley C. Livezey[1]

Abstract.—A cladistic analysis of the stiff-tailed ducks (Anatidae: Oxyurini) was conducted using 92 morphological characters. The analysis produced one minimum-length, completely dichotomous phylogenetic tree of high consistency (consistency index for informative characters, 0.74). Monophyly of the tribe was supported by 17 unambiguous synapomorphies. Within the tribe, *Heteronetta* (1 species) is the sister-group of other members; within the latter clade (supported by 21 unambiguous synapomorphies), *Nomonyx* (1 species) is the sister-group of *Oxyura* (6 species) + *Biziura* (1 species). The latter clade is supported by 10 unambiguous synapomorphies. Monophyly of *Oxyura* proper is supported by three unambiguous synapomorphies. All branches in the shortest tree except that uniting *Oxyura,* exclusive of *jamaicensis,* were conserved in a majority-rule consensus tree of 1000 bootstrapped replicates. *Biziura* and (to a lesser extent) *Heteronetta* were highly autapomorphic. Modest evolutionary patterns in body mass, reproductive parameters, and sexual dimorphism are evident, with the most marked, correlated changes occurring in *Heteronetta* and (especially) *Biziura.* The implications of these evolutionary trends for reproductive ecology and biogeographic patterns are discussed, and a phylogenetic classification of the tribe is presented. *Received 27 April 1994, accepted 10 Nov. 1994.*

The stiff-tailed ducks (Anatidae: Oxyurini) include some of the most distinctive species of waterfowl; among its members are the only obligate nest-parasite (Black-headed Duck; *Heteronetta atricapilla*) and the species showing the greatest sexual size dimorphism (Musk Duck; *Biziura lobata*) in the order Anseriformes (Delacour 1959; Johnsgard 1962, 1978; Weller 1968; Livezey 1986). Members of the Oxyurini are foot-propelled diving birds (Townsend 1909, Brooks 1945, Tome and Wrubleski 1988) and range in diving ability from the largely surface-feeding Black-headed Duck to the highly specialized Musk Duck (Raikow 1970, 1973; Livezey 1986). Stiff-tailed ducks generally inhabit freshwater lakes and marshes, typically construct over-water nests, and occur in most major land areas worldwide (Delacour 1959; Weller 1964a–d; Johnsgard 1978).

Since the reclassification of the White-backed Duck (Dendrocygninae: *Thalassornis leuconotus*) on behavioral and morphological grounds (Johnsgard 1967; Raikow 1971; Livezey 1986, 1995), systematic controversies concerning the stiff-tailed ducks have focused on the tribal position of the Black-headed Duck, currently considered to be a comparatively primitive member of the Oxyurini (e.g., Salvadori 1895; Phillips 1925, 1926; Peters 1931; Boetticher 1942, 1952; Delacour and Mayr 1945; Ver-

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heyen 1953; Delacour 1959; Johnsgard 1961a, 1965a, 1978; Rees and Hilgarth 1984; Livezey 1986; Sibley and Monroe 1993). Intergeneric relationships within the tribe were considered explicitly by Johnsgard (1961a; figs. 8, 9), who depicted *Heteronetta* as the sister-group of *Oxyura* and *Biziura*.

Species of *Oxyura* have been grouped, either by implication through the taxonomic sequences (Salvadori 1895; Phillips 1926; Peters 1931; Boetticher 1942, 1952; Delacour 1959; Wolters 1976) or by explicit argument or diagram (Delacour and Mayr 1945; Johnsgard 1961a, 1965a, 1967, 1968), as follows: (1) the unusual Masked Duck ("*O.*" *dominica*) of the neotropics, segregated in the monotypic genus *Nomonyx* by some (Salvadori 1895, Phillips 1926, Peters 1931, Woolfenden 1961, Livezey 1986); (2) the Northern Ruddy Duck (*O. jamaicensis*; sometimes including the Peruvian Ruddy Duck, *O. ferruginea*) and White-headed Duck (*O. leucocephala*) of the northern hemisphere; and (3) the variously partitioned and ranked southern-hemisphere forms (Argentine Ruddy Duck, *O. vittata*; Maccoa Duck, *O. maccoa*; Blue-billed Duck, *O. australis*; and Peruvian Ruddy Duck, *O.* [*jamaicensis*] *ferruginea*). Johnsgard (1966) described particular behavioral similarities between the Blue-billed Duck of Australia and the Argentine Ruddy Duck of southern South America. In two later works, Johnsgard (1978, 1979) proposed that the White-headed Duck was more closely related to the Maccoa Duck than to the Northern Ruddy Duck. The status and relationships of the Peruvian Ruddy Duck and the Colombian Ruddy Duck remain controversial (Delacour and Mayr 1945; Delacour 1959; Johnsgard 1961a, 1965a, 1967, 1968, 1978, 1979; Siegfried 1976; Adams and Slavid 1984).

An understanding of the marked evolutionary patterns in this unique group of waterfowl is contingent on a proposal of a robust, explicit phylogenetic hypothesis. This paper presents a species-level phylogenetic (cladistic) analysis of the stiff-tailed ducks, using morphological characters. This analysis is followed by an examination of evolutionary trends in selected life-history traits in the context of the phylogeny presented. Biogeographic issues also are considered and a phylogenetic classification of modern Oxyurini is proposed.

MATERIALS AND METHODS

Taxonomy.—As in my previous genus-level analysis of the Anseriformes (Livezey 1986), I recognize four genera in the tribe Oxyurini, of which three are monotypic: *Heteronetta, Nomonyx, Oxyura,* and *Biziura.* Opinions have varied regarding the number and composition of species to be recognized within *Oxyura* (exclusive of *dominica*); e.g., three species were recognized by Delacour and Mayr (1945), whereas Johnsgard (1961a, 1978, 1979) listed five. I adopted a conservative scheme, treating as a species any lineage diagnosable by the qualitative characters used in the phylogenetic analysis, an approach that admits a maximal

number of possible phylogenetic inferences and that is compatible with the phylogenetic species concept (Cracraft 1983, 1988). The following six species of *Oxyura* were recognized: *jamaicensis* (including *rubida*), *ferruginea, vittata, australis, leucocephala,* and *maccoa.* In addition, the *andina* population of northern South America (typically included in *O. jamaicensis*) was analyzed separately in some analyses in an attempt to assess the likelihood of its purportedly hybrid origin; the only defining character detected for *andina* is its variably black-marked, white cheeks, a character interpretable as evidence of introgression (Adams and Slavid 1984).

Definition of characters.—Characters were defined on the basis of direct examination of study skins, skeletons, and tracheae of stiff-tailed ducks and other Anatinae, as well as a review of the relevant literature (Pycraft 1906; Phillips 1925, 1926; Delacour and Mayr 1945; Delacour 1959, 1964; Johnsgard 1961b, 1962, 1965b, 1967, 1978; Humphrey and Clark 1964; Lowe 1966; Weller 1968; Siegfried 1970; Palmer 1976; Madge 1984; Torres 1984; Torres and Ayala 1986; Madge and Burn 1988; King 1989; McLelland 1989; Marchant and Higgins 1990; del Hoyo et al. 1992; Nelson 1993). The natal pattern of *O.* (*j.*) *andina* was examined using photographs of three specimens. A unique set of tracheal, esophageal, and gular diverticula in the Oxyurini, which produce the inflation of the neck during courtship in males, are confusingly described in the literature and remain incompletely known (e.g., Johnsgard 1961b, 1965a, 1967; Clark 1964; Siegfried 1976); states for these characters were based on direct examination of *Heteronetta atricapilla, Nomonyx dominicus, Oxyura jamaicensis, O. maccoa, O. australis,* and *Biziura lobata* and the few adequately detailed anatomical descriptions (Forbes 1882; Wetmore 1917, 1918, 1926, 1965; McLelland 1989).

Each character is a trait, judged to be homologous across taxa, that comprised a primitive (plesiomorphic) state and one or more derived (apomorphic) states. A total of 92 morphological characters were defined—39 skeletal characters (most after Livezey 1986), three characters of the trachea or esophagus, 10 characters of natal plumage, and 40 characters of the plumage and soft parts of adults (available from the author on request). Species for which a character state could not be ascertained were assigned a missing-datum code for that character. These character-states, together with a "hypothetical ancestor" vector (see below) compose a data matrix of dimension 10×92 (available from the author on request). Characters having more than one derived state were considered unordered unless a logical, consistent ordination by count, degree, or relative extent was evident (e.g., number of pairs of rectrices was analyzed as ordinal). Characters in which the derived state(s) were possessed by single species (autapomorphies) were included in the analysis because of the pervasive influence such differences have had on traditional classification and because this permits estimates of evolutionary divergence and phenetic differences among species.

Outgroups and polarities.—Representatives of the three other tribes of the Anatinae—Anatini, Mergini; Aythyini (*sensu* Livezey 1986, 1991)—were chosen as outgroups, in accordance with the preponderance of anatomical and behavioral evidence (e.g., Woolfenden 1961; Johnsgard 1961a, 1965a, 1978) and a phylogenetic analysis of the order (Livezey 1986). Although the inclusion of Mergini and Oxyurini in the Anatinae is reasonably well supported (Livezey 1986), the relationships among the tribes of Anatinae remain poorly resolved (Livezey, unpubl. data). Polarities (directionalities of character change) were established by ascertaining the distributions of states of each character in the other tribes of Anatinae; these states were hypothesized to be the primitive conditions (plesiomorphous states) for the characters with respect to the ingroup (Oxyurini). These individual plesiomorphous states were combined into a single vector or "hypothetical ancestor" which in turn was used to root the tree(s).

An early divergence of the Oxyurini from most other Anseriformes was proposed by

Madsen et al. (1988) and Sibley and Ahlquist (1990) and adopted by Sibley and Monroe (1990). This view (Sibley and Ahlquist 1990: fig. 357) implies that any member of the Anseriformes exclusive of the Anhimidae, *Anseranas,* and *Dendrocygna* is equally closely related to the Oxyurini, a diverse set of outgroups indeed. This proposal, however, is not considered credible in light of numerous substantive criticisms of DNA hybridization as a tool for phylogenetic inference (Cracraft 1987, Houde 1987, Sarich et al. 1989), additional irregularities in the application of the technique by Sibley and colleagues (Lewin 1988a, b; Krajewski 1991; Mindell 1992), the subjective placement of the Oxyurini within the Anseriformes and unfavorable metric properties associated with sparse data matrices (Lanyon 1992), inconsistent classificatory methodology (Siegel-Causey 1993), and the inadequate representation of the tribe in the analysis (the sole representative being one species of *Oxyura*). Other molecular studies including at least one representative of the Oxyurini, all of which also were phenetic, included too few genera or failed to resolve intergeneric relationships adequately for meaningful comparisons (Brush 1976, Patton and Avise 1985, Scherer and Sontag 1986).

P. J. Fullagar (in Marchant and Higgins 1990) suggested that the unique and primitive Freckled Duck (*Stictonetta naevosa*) is closely related to the stiff-tailed ducks, primarily on the basis of the phenetic findings of Madsen et al. (1988) and Sibley and Monroe (1990), similarities in selected behavioral and anatomical characters, and a misinterpretation of a study by Faith (1989). Although polarities of most skeletal characters used herein were unchanged, use of *Stictonetta* as the outgroup necessitated equivocal, mutually contradictory changes in polarities in seven osteological characters (*Stictonetta* exclusively sharing three with *Heteronetta,* three others with *Biziura,* and one with Oxyurini exclusive of *Heteronetta*). Also, postulation of *Stictonetta* as the sister-group of the Oxyurini required six additional changes in osteological characters shared by the Tadorninae and Anatinae (Livezey 1986), while saving only one step in the inferred polarity of the bulla syringealis. Natal characters of Oxyurini proved all but non-comparable with the unique natal pattern of *Stictonetta.* Characters of the definitive integument of Oxyurini also were difficult to compare with *Stictonetta* and require additional homoplasies in the wing speculum and tarsal scutellation in a global analysis. Pending documentation and phylogenetic analysis of the alleged similarities between *Stictonetta* and the Oxyurini mentioned by Fullagar (including the questionably homologous coloration of the maxillary rhamphotheca and undescribed details of the hemipenes) or other corroborating evidence, use of the Anatinae as the outgroup for the Oxyurini seems justified, and (for the characters analyzed here) probably of negligible topological effect within the tribe.

Derivation of trees.—Trees were derived according to the principles of phylogenetic analysis under the criterion of global parsimony (Wiley 1981). Trees were constructed using the phylogenetic software PAUP 3.1 (Swofford 1993); supplementary topological analyses, *a posteriori* character mappings, and printing of trees were performed on MacClade 3.01 (Maddison and Maddison 1992). Both programs were implemented on a Macintosh Quadra 800. I used the deterministic "branch-and-bound" algorithm to find the shortest tree(s). The character-state optimization used was accelerated transformation (ACCTRAN); employment of delayed transformation (DELTRAN) did not affect the solution set. A bootstrapping procedure using the branch-and-bound algorithm, intended as an index to empirical support for branches and not rigorous statistical inference (Felsenstein 1985, Sanderson 1989), was employed to generate 1000 topological replications. Stability of branches within the final tree was summarized by a 50% majority-rule consensus tree of these replicate trees.

Ecomorphological trends.—Selected functionally important but presumptively nonhomologous characteristics were compiled for assessment of evolutionary patterns; these attributes were mapped *a posteriori* onto the independently inferred phylogenetic tree, thereby

permitting phylogenetically based comparative analyses (Smith and Patterson 1988, Brooks and McLennan 1991, Harvey and Pagel 1991). States of these attributes–including body mass, clutch size, egg size, nesting habits, diet, and diving behavior—were taken from the literature (Delacour 1959, Schönwetter 1961, Frith 1967, Raikow 1973, Palmer 1976, Cramp and Simmons 1977, Todd 1979, Brown et al. 1982, Livezey 1986, Madge and Burn 1988, Rohwer 1988, Marchant and Higgins 1990, del Hoyo et al. 1992, Dunning 1993). Mean body masses of species were estimated by the unweighted mean of the mean masses for adults of the two sexes separately. "Sexual size dimorphism" was measured by the ratio of the mean body mass of males divided by the mean body mass of females. "Relative clutch mass" was defined by the product of mean clutch size and mean egg mass divided by the mean body mass of an adult female.

Phylogenetic classification.—The resultant phylogenetic tree(s) formed the basis for a Linnean classification that maximally reflects the relationships inferred for the ingroup. Unconventional taxonomic ranks (subtribes, supergenera, and subgenera) were based on senior taxa of appropriate rank, in part based on the classifications of Boetticher (1942, 1952) and the synonomies of Phillips (1925, 1926), Brodkorb (1964), and Wolters (1976).

RESULTS

Shortest tree.—A single, completely dichotomous, shortest tree was found for the Oxyurini, having a total length of 127, a consistency index (excluding autapomorphies) of 0.81, a retention index of 0.81, and a re-scaled consistency index of 0.71. Monophyly of the tribe is supported by 17 unambiguous synapomorphies (Fig. 1). Within the tree, *Heteronetta* is the sister-group of all other Oxyurini; the latter group (supported by 20 unambiguous synapomorphies) comprises two major subgroups—(1) *Nomonyx* and (2) *Oxyura* + *Biziura* (Fig. 1). Monophyly of the clade comprising *Oxyura* and *Biziura* is supported by 10 unambiguous synapomorphies; three unambiguous synapomorphies support the monophyly of *Oxyura.* Within *Oxyura, O. jamaicensis* is resolved to be the sister-group of its congeners. The latter clade (supported by a single synapomorphy) comprises two basic subgroups, both polyspecific (Fig. 1): (1) *O. ferruginea* and its sister-group *O. vittata* + *O. australis* (each branch supported by one synapomorphy) and (2) the sister-species *O. maccoa* and *O. leucocephala* (supported by four synapomorphies).

An analysis in which the Colombian Ruddy-Duck (*O. "andina"*) was included as a separate operational unit placed the taxon in two equally parsimonious positions within *Oxyura* exclusive of *O. jamaicensis*: (1) as the sister-group of the clade comprising the remaining *Oxyura* or (2) as a monotypic branch in a trichotomy including two other clades, *ferruginea* + *vittata* + *australis* and *maccoa* + *leucocephala.*

Apomorphic divergence.—The three monotypic genera each had several autapomorphies: *Heteronetta* (8), *Nomonyx* (5), and *Biziura* (28). The genus *Biziura* exceeds all other Anseriformes in autapomorphic divergence, both in this analysis (Fig. 1) and an earlier genus-level study (Liv-

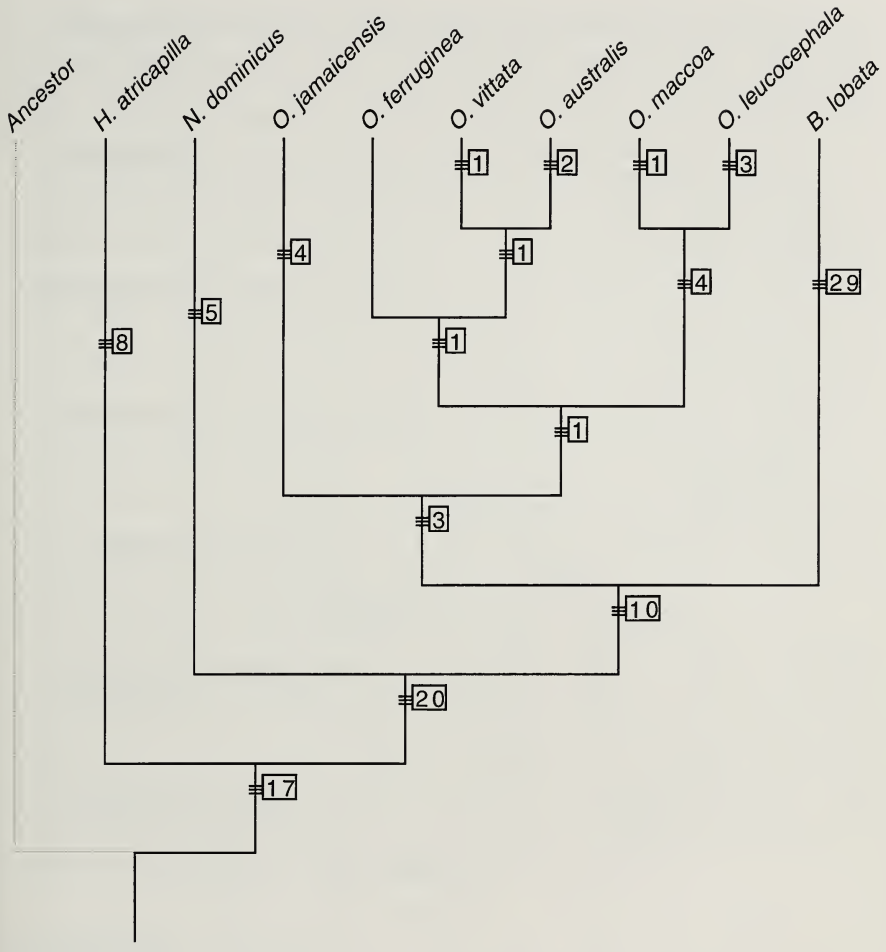

FIG. 1. Most-parsimonious phylogenetic tree for the Oxyurini based on 92 morphological characters. Numbers of unambiguous character changes supporting each branch are indicated.

ezey 1986). Within the genus *Oxyura* (excluding *Oxyura* "*andina*"), only *O. ferruginea* lacked a defining autapomorphy (Fig. 1); numbers of autapomorphies in the other five species ranged from four in *O. jamaicensis* to one each in *O. vittata* and *O. maccoa* (Fig. 1).

Robustness of tree.—Bootstrapping revealed that all branches in the shortest tree (Fig. 1), with the exception of that uniting *Oxyura* exclusive of *jamaicensis,* were conserved in a majority of replications with varying frequency (Fig. 2). The branches defining the entire tribe and uniting

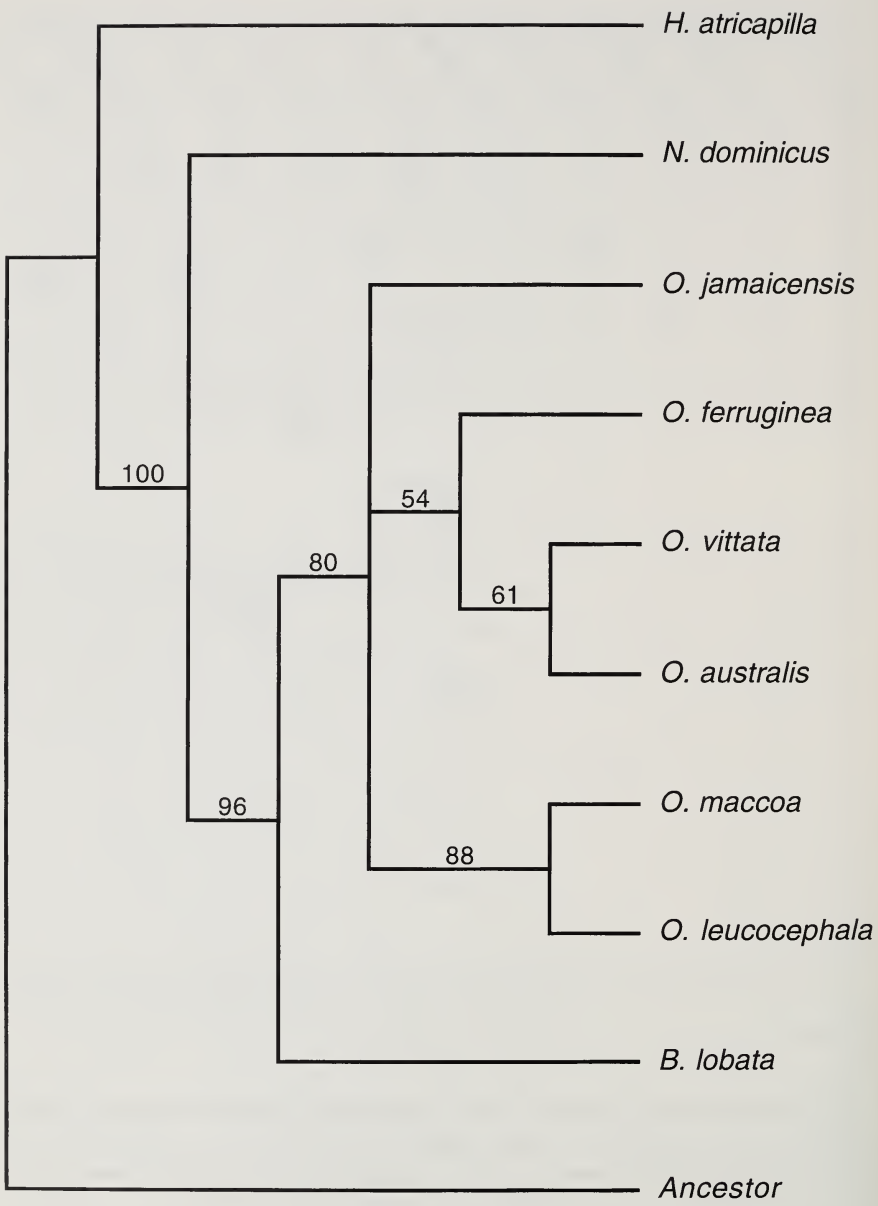

FIG. 2. Fifty-percent majority-rule consensus tree of 1000 bootstrapped replications of the shortest phylogenetic tree of the Oxyurini (Fig. 1). Percentages of replications in which each branch was conserved are indicated.

the Oxyurini exclusive of *Heteronetta* were retained in 100% of the bootstrapped replicates (Fig. 2). The branch supporting the clade comprising *Oxyura* and *Biziura* was conserved in 96% of the bootstrapped replicates. Nodes within *Oxyura* were conserved in 54–88% of the replicates (Fig. 2).

Ecomorphological patterns.—Body mass showed only moderate phylogenetic conservatism in the Oxyurini (CI = 0.60), evidently having undergone one autapomorphic decrease in *Nomonyx* and independent increases in *O. ferruginea, O. australis,* and (especially) *Biziura* (Fig. 3). Clutch size was comparable to body mass in consistency (CI = 0.67); this parameter appears to have increased in *O. jamaicensis* and to have decreased in *Biziura* and is undetermined in the strictly nest-parasitic *Heteronetta* (Fig. 4). Egg mass (CI = 0.67) evidently increased homologously in *Oxyura* exclusive of *O. jamaicensis* and independently to a greater degree in *Biziura* (Fig. 5). Taken together, these patterns in egg mass and clutch size (relative to female body mass) indicate modest, independent increases in relative clutch mass in *Nomonyx* and in two lineages of *Oxyura* (*O. jamaicensis* and in *O. maccoa* + *O. leucocephala*), and a decrease in this parameter in *Biziura* (CI = 0.60).

Sexual size dimorphism showed a moderately complex evolutionary pattern in the Oxyurini, evidently having (Fig. 6; CI = 0.60) (1) shifted to female-larger dimorphism in *Heteronetta,* (2) increased paraphyletically in *Nomonyx, O. jamaicensis,* and (especially) *Biziura,* and (3) undergone a reversal in other *Oxyura* (especially *O. australis*). Sexual dichromatism of plumage, however, showed a very different pattern, with a reduction of sexual differences in *Heteronetta* and an independent reversal to monochromatism in *Biziura* (CI = 0.60).

DISCUSSION

Phylogenetic inferences and classification.—The trees presented by Johnsgard (1961a: figs. 8, 9) are the only species-level hypotheses of the phylogeny of the Oxyurini available for comparison. The relationships depicted by Johnsgard (1961a) differ from those proposed here in three major ways: (1) the positions of "*N.*" *dominicus* and *B. lobata* were reversed, (2) *Oxyura* was partitioned into two major groups—*leucocephala* + *jamaicensis* and *vittata* + *maccoa* + *australis,* and (3) *O. ferruginea* was merged with *O. jamaicensis.* Based on the data matrix complied here, the topology proposed by Johnsgard (1961a) is 13 steps (10%) longer (less parsimonious) than the shortest tree inferred here (Fig. 1). Six of these additional steps are attributable to the inclusion by Johnsgard (1961a) of *Nomonyx* as the sister-group of *Oxyura* (instead of *Biziura*), a topology implied also by all classifications in which *dominicus* is listed

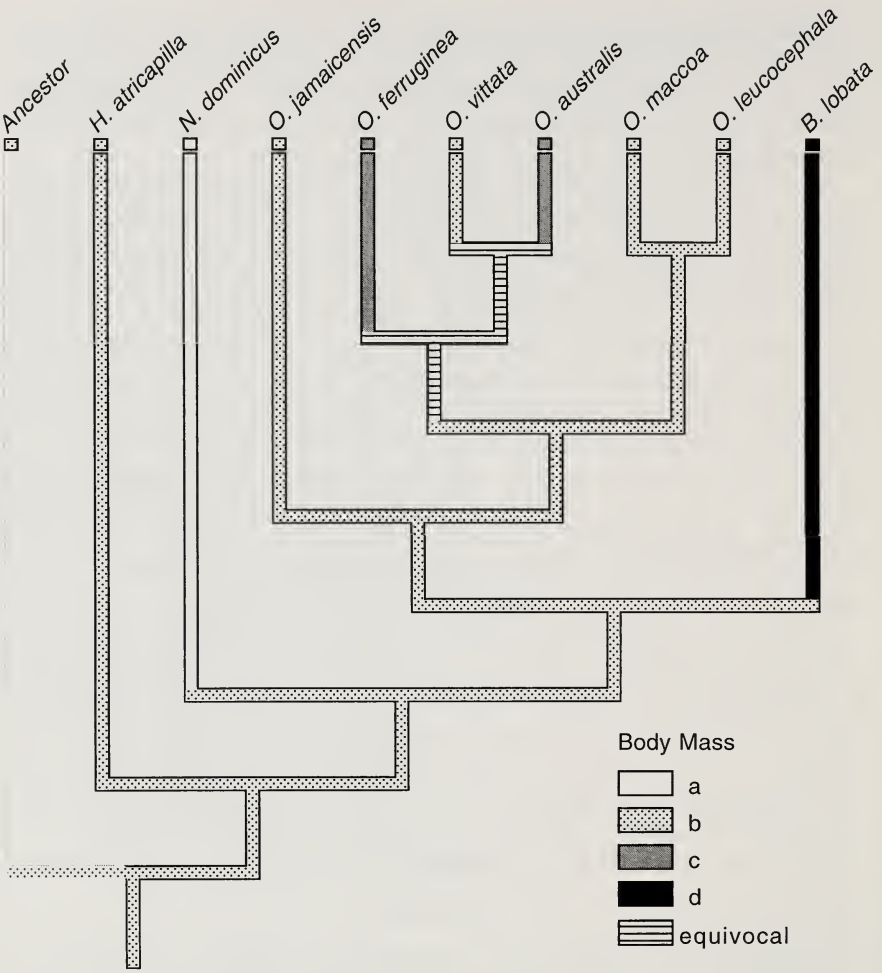

FIG. 3. Map of mean body mass (g) on phylogeny of the Oxyurini (primitive state for tribe in boldface): a—<500, **b—500–750**, c—751–1000, d—>1000. Character descriptions and data matrix available from author on request.

first within *Oxyura* (e.g., Delacour and Mayr 1945; Delacour 1959; Johnsgard 1978, 1979). If *Biziura* is to be generically distinguished from *Oxyura* (its sister group), the present analysis requires (at least) that *Nomonyx dominicus* also be generically separated. Another classificatory recommendation deriving from the present analysis is that *O. ferruginea* not be merged with *O. jamaicensis* but instead be grouped separately with two other southern-hemisphere species (see classification in Appendix I).

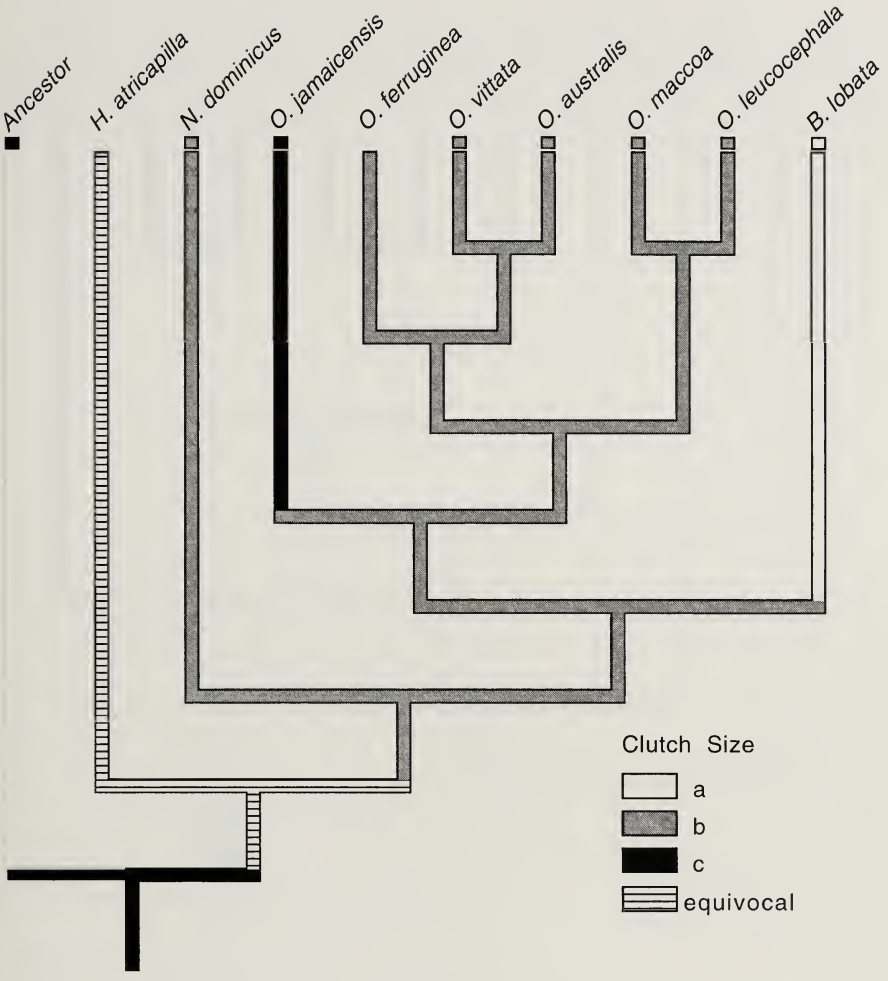

FIG. 4. Map of mean clutch size on phylogeny of the Oxyurini (primitive state for tribe in boldface): a—<3, b—3–6, **c—>6**. Character descriptions and data matrix available from author on request.

The taxonomic status of the variable *O.* (*j.*) *andina* remains unresolved, and its purported hybrid status deserves intensive study; it is merged provisionally with *O. jamaicensis*. Moreover, if *O.* (*j.*) *andina* were to be confirmed to be a hybrid swarm between *O. jamaicensis* and *O. ferruginea,* no reliable inferences concerning the phylogenetic relationship between the two "parent" forms could be made. Although propensity for interspecific hybridization traditionally has been considered to be pre-

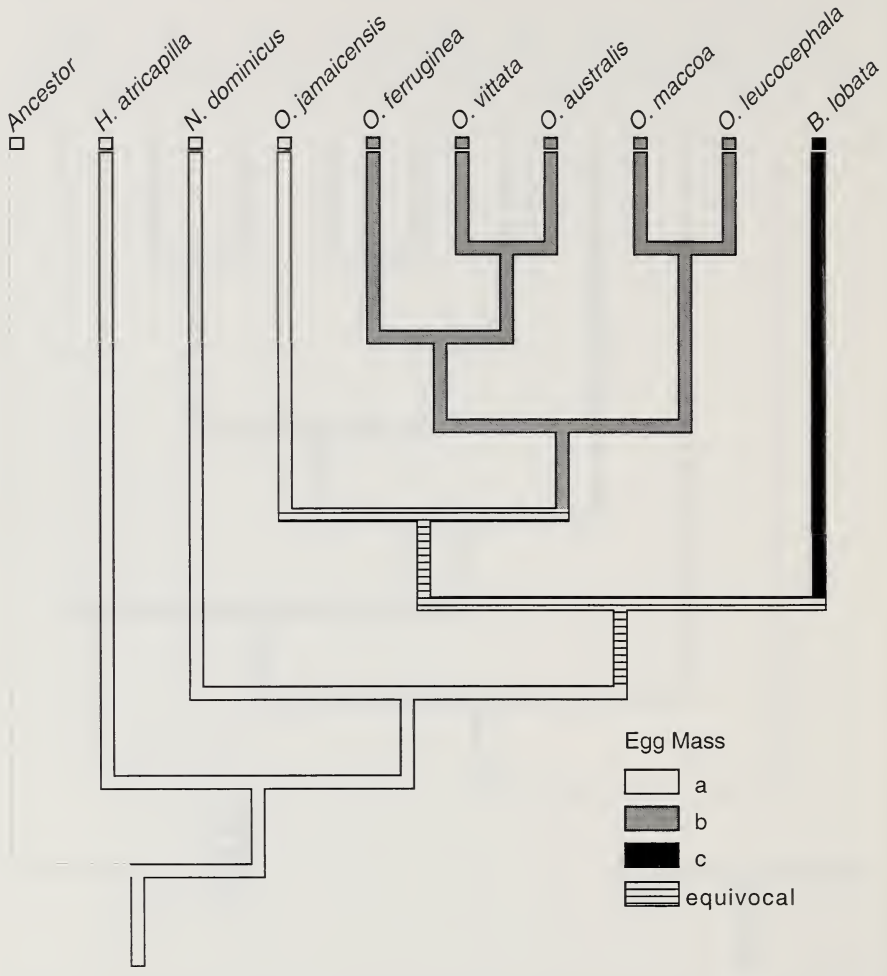

FIG. 5. Map of mean egg mass (g) on phylogeny of the Oxyurini (primitive state for tribe in boldface): **a—50–75**, b—76–100, c—>100. Character descriptions and data matrix available from author on request.

vented by adaptive "isolating mechanisms" and to indicate closeness of phylogenetic relationship (Sibley 1957; Johnsgard 1960b, 1963), interspecific hybridization instead reflects the retention of primitive interfertility subsequent to speciation, and therefore this symplesiomorphy provides no direct evidence of relatedness (Livezey 1991). Furthermore, the great diversity of recorded interspecific, intergeneric, and intertribal hybrids among Anseriformes further undermines any evolutionary insights

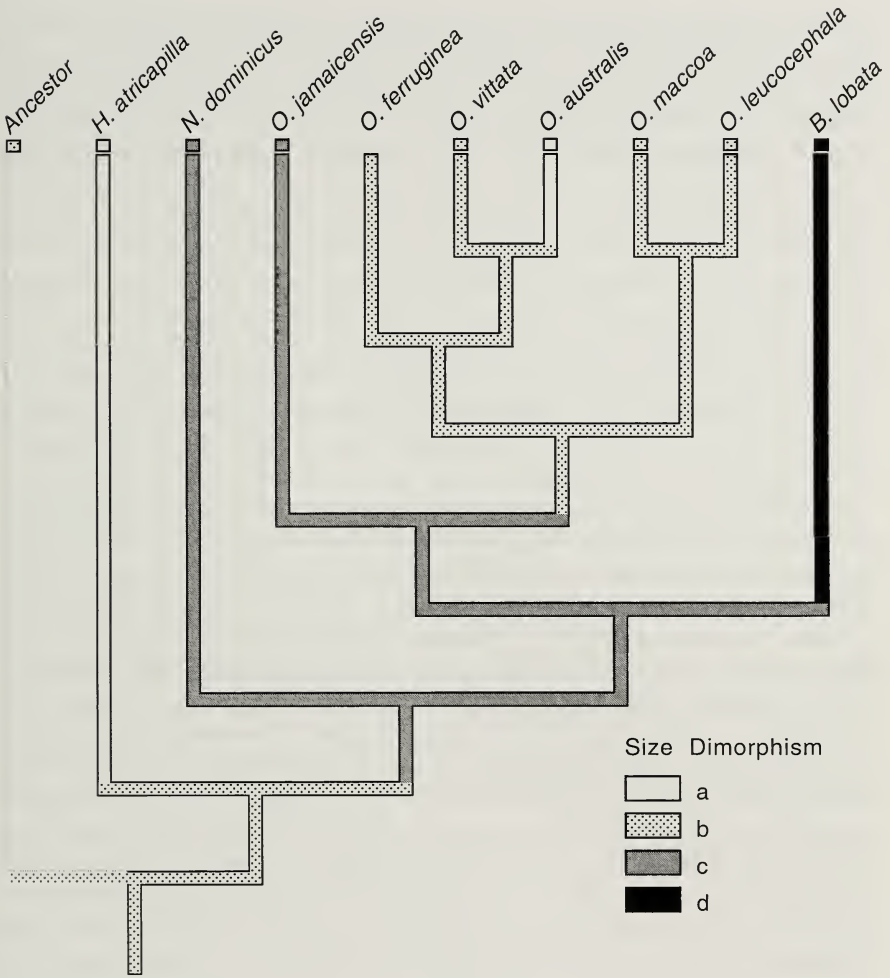

FIG. 6. Map of sexual size dimorphism (ratio of means [g] for sexes) on phylogeny of the Oxyurini (primitive states for tribe in boldface): a—<1.00, **b—1–1.15**, c—1.16–1.30, d—>1.30. Character descriptions and data matrix available from author on request..

to be gained from patterns of hybridization (Johnsgard 1960b, Scherer and Hilsberg 1982).

Evolutionary trends.—Of the several quantitative parameters mapped onto the phylogenetic tree for the Oxyurini, probably the most distinct patterns emerged for egg mass (Fig. 5). The general increase in absolute egg mass evident in the tribe (Fig. 5), coincident with a general decrease in clutch size (Fig. 4), conforms with a weak, inverse relationship between

sizes of eggs and clutches in Anseriformes (Lack 1967, Rohwer 1988). Egg masses predicted by the equation of Rahn et al. (1975) relating egg mass to female body mass for the Anseriformes confirm that the egg masses of Oxyurini are large relative to the corresponding mean body masses of females (Lack 1967, Briggs 1988). The combination of small clutch size and large (absolute) egg size in the Oxyurini resembles that of many insular species of dabbling ducks (Anatini; Livezey 1990, 1993), but clearly the selection regimes of the latter differ significantly from those shared by the Oxyurini (Weller 1964a–c). Moreover, two comparatively massive species of Oxyurini—*Oxyura australis* and *Biziura lobata*—have relative egg masses typical of most Anatini, whereas egg size in most insular endemics is especially high relative to body mass (Livezey 1993). Unfortunately, the proportion of egg mass composed of yolk, a relationship with important implications for growth rates, is not known for the Oxyurini (Lack 1968).

In addition to the complex changes in body mass, general decreases in clutch size, and changes in egg mass evident in the Oxyurini (Fig. 5), evolutionary patterns in several other aspects of the life-history of the stiff-tailed ducks can be inferred in the context of the phylogenetic hypothesis proposed here (Fig. 1). Sexual dichromatism underwent reduction or loss in two very different lineages but manifests little correlation with sexual size dimorphism (Fig. 6). Comparatively inconspicuous sexual differences color of plumage and soft parts characterize *Heteronetta,* an obligate nest parasite showing modest female-larger size dimorphism (Weller 1967, 1968; Maynard Smith 1977), and the virtually monochromatic *Biziura,* a polygynous species showing extreme male-larger size dimorphism (Frith 1967, Livezey and Humphrey 1984). Infrequent nest parasitism evidently characterizes all other Oxyurini and is probably plesiomorphous in the Anatinae (Attiwill et al. 1981, Eadie et al. 1988, Rohwer and Freeman 1989). The Oxyurini exclusive of *Heteronetta* also share a moderate tendency toward (at least infrequent) crepuscular or nocturnal feeding, a habit perhaps most developed in *Nomonyx* (Weller 1968, McNeil et al. 1992).

The courtship displays of the Oxyurini include several distinctive behaviors, although the behaviors of several species remain inadequately known (Delacour 1959; Johnsgard 1960a, 1961a, 1962, 1965a, 1978). Males of at least *Nomonyx* and *Oxyura* perform unique displays involving the rapid thumping of the bill on the inflated throat sac(s); other displays that unite males of most Oxyurini include "tail cocking," "bill dipping," various surface rushes, and "sousing" (Johnsgard 1961a, 1962, 1965a, b, 1966, 1967, 1968, 1978; Fullagar and Carbonell 1986). Male Musk Ducks perform bizarre courtship displays, which typically involve a number of

acoustically and visually conspicuous components, including "paddling kicks," "whistle kicks," "plonk kicks," and exhibition of the fleshy gular lobe or palear (Johnsgard 1965a, 1966, 1967; Frith 1967; Fullagar and Carbonell 1986). Females of the Oxyurini, including *Heteronetta,* lack the "decrescendo" and "inciting" vocalizations that characterize female Anatini.

Biogeographic patterns.—Modern members of the Oxyurini are limited in distribution to the Neotropics, southern Nearctic, southern Africa, the Mediterranean, central Palearctic, and southern Australia (Weller 1964d). Fossils of the tribe are limited to a few weakly differentiated forms from these same regions that were assignable to modern genera (Brodkorb 1964, Howard 1964). Subfossil remains merely extend the former ranges of the two Australian members—*O. australis* and *B. lobata*—to New Zealand (Brodkorb 1964, Horn 1983).

The phylogenetic hypothesis proposed here strongly indicates a southern-hemispheric origin for the tribe, in that the two deepest branches (*Heteronetta* and *Nomonyx*) are Neotropical in distribution, and the next earliest branch (*Biziura*) is Australian (Fig. 1). Within *Oxyura,* the first branch corresponds to a northern-hemisphere species (*jamaicensis*), with the remaining members grouped into Palearctic-African (*maccoa* and *leucocephala*) and Neotropical-Australian clades (*ferruginea, vittata,* and *australis*). A strict vicariance model for the Oxyurini, in which a nested subdivision of regions corresponds with phylogenetic patterns, is not possible for extant species (Fig. 1). The complete absence of insular populations of Oxyurini suggests that members of the tribe, although most are migratory, are among the poorest dispersers in the Anseriformes (Weller 1964a). Field observations substantiate the poor flying abilities of most Oxyurini (Johnsgard 1978). Musk Ducks have especially high wing-loadings (Frith 1967), and large males not in wing molt may be at least temporarily flightless (Goodwin 1974, Marchant and Higgins 1990). The lack of insular isolates in the Oxyurini, however, may be related as much to the freshwater habitats of the member species (Weller 1964b, c), a preference that would deter trans-oceanic migration and insular colonization.

Evolutionary anomalies of the Musk Duck.—The Musk Duck, in addition to its unusual courtship displays, is unique among Oxyurini in its comparatively huge body size, highly autapomorphic skeletal anatomy, predominantly animal diet, frequency of maternal feeding of young, delayed sexual maturation (two years of age), lack of pair-bonds and associated "promiscuous" or polybrachygynous mating system, absence of sexual dichromatism of plumage, extreme sexual size dimorphism, dark natal plumage (Fig. 7), and small clutch size (Frith 1967; Johnsgard

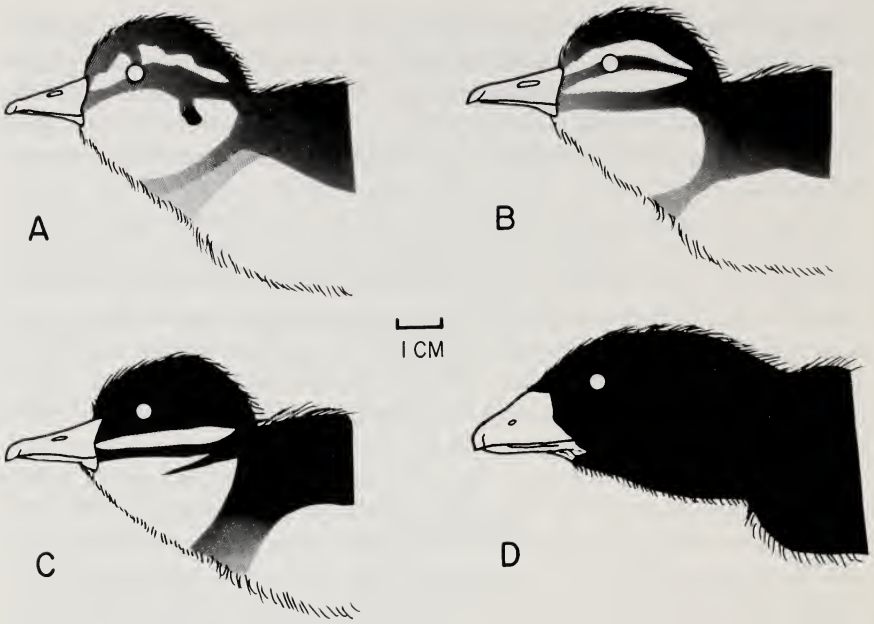

FIG. 7. Plumage patterns of natal Oxyurini, lateral views: A—*Heteronetta atricapilla* (USNM 337995); B—*Nomonyx dominicus* (AMNH 2240); C—*Oxyura jamaicensis* (USNM 259366); and D—*Biziura lobata* (AMNH 734131).

1965a, b, 1966, 1978; Kear 1970; Livezey 1986). The association of exaggerated sexual size dimorphism with low parental investment by males in *Biziura* conforms with broad patterns documented for birds (Selander 1972, Trivers 1972, Payne 1984; but see Höglund 1989), but this association is comparatively weak among waterfowl generally (Sigurjónsdóttir 1981). Similarly, the coincidence of the loss of sexual dichromatism with polygyny in *Biziura* opposes general avian patterns (Butcher and Rohwer 1989) but conforms with the comparatively poor correspondence between plumage dimorphism and paternal investment in Anseriformes (Sigurjónsdóttir 1981, Scott and Clutton-Brock 1989). The unique gular lobe or palear in male *Biziura,* and its use in courtship, performs some of the advertising functions of bright plumage (Frith 1967; Johnsgard 1965a, b, 1966). The possible role of the seasonally pungent uropygial secretions of male *Biziura,* if any, remains obscure (Frith 1967).

Magnitude of sexual size dimorphism is weakly associated with body size in some avian groups (Reiss 1986), but the sexual size differences of *Biziura* exceeds that attributable to the comparatively large body size of the species. The importance of body size to thermodynamics, metab-

olism, energy requirements, survivorship, and reproductive investment is profound, therefore, the evolutionary trade-offs implicit in the increased body size of male Musk Ducks (and other ecological peculiarities) deserve detailed study, especially within a phylogenetic context (Fig. 1) and with special attention to comparisons involving the partly sympatric *O. australis*.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation grants BSR-8515523, BSR-9129545, and BSR-9396249, as well as collection visitation grants from the National Museum of National History (USNM) and the American Museum of Natural History (AMNH). The generous hospitality of G. Mack and R. L. Zusi made several prolonged visits to New York and Washington productive and enjoyable. I am grateful for loans and/or access to collections provided by the curatorial personnel of the following institutions: Division of Birds, National Museum of Natural History; Department of Ornithology, American Museum of Natural History; Division of Birds, Museum of Zoology, University of Michigan; Division of Birds, Field Museum of Natural History; Sub-department of Ornithology, British Museum of Natural History; Wildfowl and Wetlands Trust; and Division of Ornithology, Museum of Natural History, University of Kansas. M. Brown (Wildfowl and Wetlands Trust) examined tracheae and esophagi of several Oxyurini, and F. G. Stiles (Institut de Ciencias Naturales, Universidad de Colombia) kindly provided photographs of three natal *Oxyura (j.) andina*. I also thank P. S. Humphrey, R. F. Johnston, D. Siegel-Causey, L. Trueb, and E. O. Wiley for a variety of helpful inputs, and P. A. Johnsgard and R. O. Prum made helpful comments on the manuscript.

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APPENDIX I

CLASSIFICATION OF OXYURINI

Tribe Oxyurini Delacour & Mayr, 1945.—Stiff-tailed ducks.
Subtribe Heteronetteae Boetticher, 1952.
Genus *Heteronetta* Salvadori, 1865.
Heteronetta atricapilla (Merrem, 1841).—Black-headed Duck.
Subtribe Oxyureae Boetticher, 1942.—True stiff-tailed ducks.
Supergenus *Nomonyx* Ridgway, 1880.
Genus *Nomonyx* Ridgway, 1880.
Nomonyx dominicus (Linnaeus, 1766).—Masked Duck.
Supergenus *Oxyura* Bonaparte, 1828.—Typical stiff-tailed ducks.
Genus *Oxyura* Bonaparte, 1828.
Subgenus *Oxyura* Bonaparte, 1828 (>*Erismatura* Bonaparte, 1832).
Oxyura jamaicensis (Gmelin, 1789).—Northern Ruddy Duck.
Subgenus *Cerconectes* Wagler, 1832.
Species-group "A."
Oxyura ferruginea (Eyton, 1838).—Peruvian Ruddy Duck.
Oxyura vittata (Philippi, 1860).—Argentine Ruddy Duck.
Oxyura australis (Gould, 1836).—Blue-billed Duck.
Species-group "B."
Oxyura maccoa (Eyton, 1836).—Maccoa Duck.
Oxyura leucocephala (Scopoli, 1796).—White-headed Duck.
Genus *Biziura* Stephens, 1824.
Biziura lobata (Shaw, 1796).—Musk Duck.

Wilson Bull., 107(2), 1995, pp. 235–250

MORPHOLOGICAL AND GENETIC DIVERGENCE AMONG ALASKAN POPULATIONS OF *BRACHYRAMPHUS* MURRELETS

JAY PITOCCHELLI,[1,2] JOHN PIATT,[3] AND MATTHEW A. CRONIN[3,4]

ABSTRACT.—We studied morphological and mitochondrial DNA (mtDNA) divergence among three populations of *Brachyramphus* Murrelets: Kittlitz's Murrelets (*B. brevirostris*), and tree-nesting and ground-nesting Marbled Murrelets (*B. marmoratus*). We found little morphological divergence in external and skeletal measurements among Marbled Murrelets, but both populations were easily distinguished from Kittlitz's Murrelets. Principal components analysis (PCA) of external measurements showed that Kittlitz's Murrelets occupied a distinct cloud in multivariate space separate from Marbled Murrelets. However, tree-nesting and ground-nesting Marbled Murrelets were indistinguishable. We obtained the same pattern from PCA of skeletal dimensions. Analysis of mtDNA revealed an estimate of sequence divergence of 4.4%–5.0% between Marbled Murrelets and Kittlitz's Murrelets, suggesting a divergence of about 2.2 MYBP. The difference between ground- and tree-nesting murrelets was 0.03%. This analysis suggests little divergence has occurred between tree- and ground-nesting populations of Marbled Murrelets. *Received 14 March 1994, accepted 1 Nov. 1994.*

The genus *Brachyramphus* currently contains two species of murrelets. Both are unique among the Alcidae in that they have cryptic alternate plumage and nest mostly inland instead of on predator-free, offshore islands. Kittlitz's Murrelets (*B. brevirostris*) nest on the ground in high-altitude alpine habitats throughout glaciated regions of Alaska (Van Vleit 1993). The North American subspecies of the Marbled Murrelet (*B. m. marmoratus*) breeds along the coast of the Pacific Ocean from central California to the Aleutian Islands (Carter and Morrison 1992). Over 65% of the North American population of Marbled Murrelets is found in Alaska (Piatt and Ford 1993). Throughout their range, most Marbled Murrelets nest on branches of trees in old-growth coastal forests. But in Alaska, at least 3% of the population nests on the ground in the Aleutian Islands, along the Alaskan Peninsula, and nonforested regions of coastal Alaska (Mendenhall 1992, Piatt and Ford 1993).

Tree-nesting populations of Marbled Murrelet are threatened by logging of old-growth forests, oil pollution, and gillnet fisheries through much of the breeding range (Piatt et al. 1990, Carter and Morrison 1992). Con-

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sequently, the U.S. Fish and Wildlife Service and the Canadian Wildlife Service have listed this species as "threatened" in California, Oregon, Washington, and British Columbia (Carter and Morrison 1992, Stein and Miller 1992). Despite these listings, there have been no thorough studies of genetic subdivision or geographic variation (*sensu* Zink and Remsen 1986) among Marbled Murrelet populations. Studies of morphological and genetic divergence among or within species provide crucial information about the existence of conservation units or interesting patterns within species such as clines, recent range extensions, or hybrid contact (Barrowclough 1992). Information on morphological divergence and genetic subdivision of Marbled Murrelet populations is essential to management decisions concerning the status of its widely distributed breeding populations. For example, the Asian subspecies of the Marbled Murrelet (*B. m. perdix*) has recently been elevated to a new species based on studies of mitochondrial DNA (mtDNA; Vicki Friesen, unpubl. data), effectively removing this population from management considerations for the North American populations of *B. m. marmoratus*. North American murrelets deserve special attention, especially disjunct breeding populations such as tree- and ground-nesting populations in Alaska. Results of these analyses can be used for comparisons with more contiguous southern populations experiencing recent declines.

In this paper, we examine the extent of morphological and genetic divergence between ground-nesting and tree-nesting populations of Marbled Murrelets from Alaska. These markedly different breeding behaviors may reflect invasion of new niches or adaptive zones. Genetic divergence often accompanies the exploitation of new niches. We investigated morphological divergence by comparing external measurements and skeletal dimensions of ground- and tree-nesting murrelets. Berger (1952) found that terrestrial species of cuckoos diverged from their arboreal relatives, especially in the distal elements of the hindlimb. Ground-dwelling species also tend to have stout hindlimbs for walking and running compared to their closest relatives. This is reflected among the Alcidae, in which puffins represent the extreme in ambulatory adaptation with heavy joints and long leg bones, whereas Marbled Murrelets have the shortest leg bones of any Alcids—presumably an adaptation for nesting in trees (Storer 1945). We paid close attention to variation in hindlimb measurements among ground- and tree-nesting Marbled Murrelets. We also used mtDNA to analyze genetic differences between these populations. Kittlitz's Murrelet was used as an outgroup for the morphological and genetic analyses.

STUDY AREA AND METHODS

Field work.—We used data from specimens collected during the Outer Continental Shelf Environmental Assessment Program (OCSEAP) of the 1970's and birds we collected from

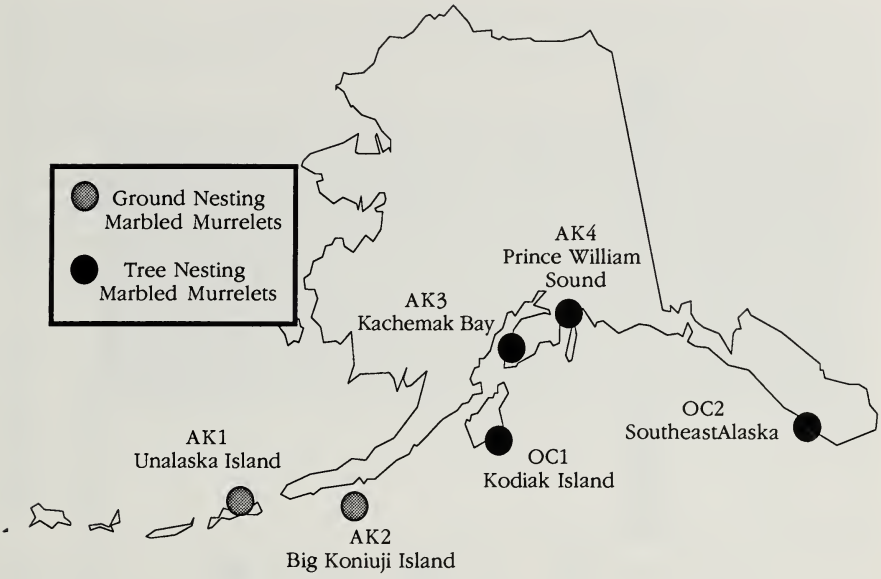

FIG. 1. Collection localities in Alaska: AK1—Unalaska Island, Captain's Bay (ground-nesting Marbled and Kittlitz's murrelets); AK2—Big Koniuji Island, Flying Eagle Harbor (ground-nesting Marbled and Kittlitz's murrelets); AK3—Kachemak Bay, Tutka Bay to Grewingk Glacier (tree-nesting Marbled and Kittlitz's murrelets); AK4—Prince William Sound, Unakwik Fjord (tree-nesting Marbled Murrelets); OC1—OCSEAP collections around the Kodiak Archipelago (tree-nesting Marbled Murrelets); OC2—collections from Glacier Bay and surrounding region (tree-nesting Marbled Murrelets). AK designations refer to collections made in the late 1980s and early 1990s while OC designations refer to OCSEAP collections of the 1970s.

1988–1992 (Fig. 1). All specimens were collected during the breeding season. Birds from the later collections were prepared as skeletal specimens in the field. Heart, liver, and breast muscle tissues from these birds were frozen in liquid nitrogen within four hours of collection. Tissues are currently stored in ultra-cold freezers at the American Museum of Natural History, New York, and at the National Biological Survey regional office in Anchorage, Alaska. Skeletal materials have been deposited at the American Museum of Natural History.

We made comparisons between three groups: tree-nesting Marbled Murrelets, ground-nesting Marbled Murrelets, and ground-nesting Kittlitz's Murrelets. Marbled Murrelet specimens collected during the breeding season from treeless areas (Aleutian and Shumagin Islands) were lumped into the ground-nesting category, whereas Marbled Murrelet specimens from the Kodiak Archipelago, Kachemak Bay, Prince William Sound, and southeast Alaska were presumed to belong to tree-nesting populations (Fig. 1). There are reported cases of ground-nesting Marbled Murrelets in southcentral and southeast Alaska, but the majority of Marbled Murrelets collected from Kodiak to southeast Alaska are assumed to be ground-nesters based on the observed distribution of known tree-nests in Alaska (Naslund et al. 1994). Breeding Kittlitz's Murrelets were collected during the OCSEAP surveys and recent collections we made in Kachemak Bay and the Aleutian and Shumagin islands.

We acknowledge that there may be different variance components, including sex, age,

and geography, that account for part of the measurement variation we observed (Baker 1985, Zink and Remsen 1986). Preliminary results of Student's *t*-tests (Pitocchelli et al., unpubl. data) revealed no significant sexual dimorphism for 13 of 18 measurements, so we pooled male and female specimens for these analyses. Only adult specimens were used. Lack of adequate skeletal materials in existing museum collections was an important factor limiting the geographic extent of our analyses.

Morphometrics.—We analyzed size variation in weight, external measurements and skeletal dimensions. We obtained data on weight and five external measurements from the OCSEAP surveys: WING—wing chord; TARS—tarsus length; CULMEN—culmen length; GAPE—gape; BDEPEXT—bill depth. Birds were weighed with Pesola scales to the nearest gram. External measurements were made with Vernier calipers to the nearest 0.1 mm.

We measured 17 skeletal dimensions from specimens collected from 1988–1992: six cranial dimensions, PRL—premaxillary length, SKW—skull width, SKL—skull length, BDEP—bill depth, MANDL—mandible length, DIAM—diameter of the sclerotic ring; 11 postcranial dimensions, CORL—coracoid length, STERL—sternum length, KEEL—keel length, KEED—keel depth, SYNMAX—maximum synsacrum width, FEL—femur length, TIBL—tibiotarsus length, TARL—tarsometatarsus length, HUML—humerus length, ULNL—ulna length, CARPL—carpometacarpus length. Measurements were entered directly into personal computers using Max-cal digital calipers and Lessoft (Marcus 1982). Measurements were made to the nearest 0.1 mm.

We carried out univariate and multivariate analyses to assess size differences among *Brachyramphus* populations. At the univariate level, we examined the contribution of species (Marbled versus Kittlitz's), sex, and individual variation to the total variance in each measurement using a Nested ANOVA (PROC NESTED, SAS 1985). We conducted an ANOVA (PROC GLM, SNK, SAS 1985) on each measurement to detect significant differences between ground-nesting Marbled Murrelets, tree-nesting Marbled Murrelets, and Kittlitz's Murrelets. A Student-Newman-Keuls post hoc comparisons test was used to determine which of the three groups were significantly different from each other.

At the multivariate level we used principal components analysis (PROC PRINCOMP, SAS 1985) to determine whether ground-nesting Marbled Murrelets, tree-nesting Marbled Murrelets, and Kittlitz's Murrelets occupy separate clouds in multivariate space. Separate PCA's were performed on the external and skeletal data. Specimens with broken bones were excluded from the PCA of skeletal measurements. We used 10 of the 17 skeletal dimensions for this analysis—SKW, CORL, STERL, KEEL, KEED, FEL, TIBL, TARL, ULNL, CARPL. We chose these characters in order to increase sample sizes while still sampling at least one bone from the skull, girdle, wing and leg complexes. Raw data were $\log_{10}$-transformed before entry into the PCA. We extracted PC scores from a variance-covariance matrix for the first two components and plotted specimens along these axes. We compared character loadings on the PC axes to determine which measurements contributed most to the separation of specimens. Character loadings are correlations between the skeletal measurements and the principal components generated by the PCA (Schnell et al. 1985).

mtDNA analysis.—We analyzed mtDNA from five Kittlitz's Murrelets, five tree-nesting Marbled Murrelets from Kachemak Bay, and nine ground-nesting Marbled Murrelets from the Shumagin Islands. We also analyzed mtDNA from two Black-legged Kittiwakes (*Rissa tridactyla*) as a distantly related outgroup. MtDNA restriction fragment patterns were compared visually and genotypes defined by composite fragment patterns (Lansman et al. 1981). MtDNA sequence divergence among genotypes (base substitutions per nucleotide, *P*) was estimated from the proportion of shared restriction fragments (F, Upholt 1977).

MtDNA variation was assessed with restriction enzymes. Genomic DNA was extracted from about 0.5 g muscle tissue using standard methods (Cronin et al. 1991a). About 0.5 μg

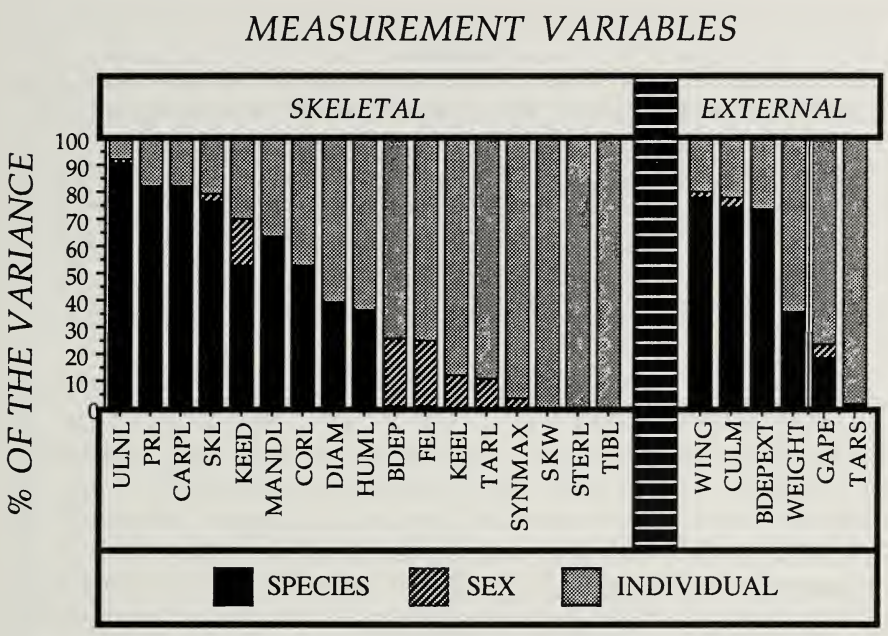

FIG. 2. Contribution of species, sex, and individual variation to character variance in a nested ANOVA of skeletal and external characters. Shaded areas represent the percentage of the total variance attributed to each variance component.

of DNA from each bird was digested with restriction enzymes (*Eco*RI, *Hin*dIII, *Pst*I, *Pvu*II, *Sac*I, *Xba*I, *Eco*RV, *Bgl*I, and *Bcl*I). Digested DNA fragments were separated electrophoretically in 0.75% agarose gels with Tris-borate-EDTA buffer (Sambrook et al. 1989), transferred onto nylon membranes by southern blotting, and the filters were baked at 80° C for 2 h. Filtrates were prehybridized at 60–65° C in 5× SSC, 1% sodium sarkosyl, 1× Denhardt's solution, 0.025 M potassium phosphate, 0.025 mg/ml salmon sperm DNA for 1 h. A [P32]-labeled mtDNA probe was denatured at 100° C and added to the prehybridization solution. The probe consisted of Northern Pintail (*Anas acuta*) mtDNA isolated from brain (see Cronin et al. 1988) and further purified in low melting agarose (Sambrook et al. 1989). Hybridization was at 60–65° C for 12–48 h with constant shaking. After hybridization, filtrates were washed for 30 min at room temperature with 2× SSC, 0.2% SDS, 1× Denhardt's solution, and two hours at 37°C with 2× SSC, 0.1% SDS. Filtrates were air dried, covered in plastic wrap, and exposed to X-ray film for 12–170 h.

RESULTS AND DISCUSSION

Morphometrics.—A nested ANOVA of external and skeletal dimensions revealed that the percentage of total variance attributable to species, sex, and individual variation was different for each mensural character (Fig. 2). Species affinity or individual variance components were responsible for most of the variation in each measurement. Species affinity ac-

TABLE 1

RESULTS FROM ANOVA OF DIFFERENCES IN EXTERNAL MEASUREMENTS FROM TREE-NESTING MARBLED MURRELETS, GROUND-NESTING MARBLED MURRELETS AND GROUND-NESTING KITTLITZ'S MURRELETS[a]

Character	Marbled Murrelet (tree)	Marbled Murrelet (ground)	Kittlitz's Murrelet (ground)	Significance
WEIGHT	225.38	225.10	241.14	0.0033
(N, SD)	171, 23.59	56, 20.33	28, 25.29	
WING	128.35	132.35	142.00	0.0001
(N, SD)	140, 5.93	14, 6.99	17, 7.36	
TARS	17.92	17.40	17.70	ns
(N, SD)	138, 1.36	12, 0.85	18, 1.91	
CULMEN	16.00	15.08	11.85	0.0001
(N, SD)	134, 1.56	12, 1.44	20, 1.30	
GAPE	34.62	32.91	32.42	0.0028
(N, SD)	32, 1.86	12, 2.50	14, 2.20	
BDEPEXT	5.97	5.93	5.12	0.0001
(N, SD)	125, 0.38	14, 0.31	14, 0.22	

[a] Means that are underlined are not significantly different from each other according to SNK post hoc comparisons test.

counted for 73% or more of the variance in three of six external measurements. Individual variation contributed 64% or more of the variance in the other external dimensions. Results of the skeletal analyses showed the same pattern. Species affinity accounted for more than 35% of the variance in nine of 17 skeletal dimensions. Individual variation accounted for 29% or more of the variance in 13 skeletal measurements. We also performed a nested ANOVA on Marbled Murrelets only (not shown here). Nesting habits and sexual dimorphism played minor roles in measurement variance compared to individual variation which accounted for 90% or more of the total variance in each character.

Comparisons of external measurements showed that size differences between Kittlitz's Murrelets and both Marbled Murrelet populations are much more pronounced than differences between ground- and tree-nesting populations of Marbled Murrelets (Table 1). This trend was evident in three of the six external measurements, WEIGHT, CULMEN, and BDEPEXT. An ANOVA of WEIGHT revealed that Kittlitz's Murrelets were significantly heavier than Marbled Murrelets, but there were no significant differences between ground- and tree-nesting Marbled Murrelets. Kittlitz's Murrelets were significantly smaller than Marbled Murrelets for CULMEN and BDEPEXT, but no differences were found among the Marbled

TABLE 2
LOADINGS OF EXTERNAL MEASUREMENTS ON THE FIRST THREE PRINCIPAL COMPONENTS

Character	Prin1	Prin2	Prin3
WING	−0.228	−0.002	0.550
TARS	0.172	0.825	0.465
CULMEN	0.864	−0.369	0.340
BDEPEXT	0.412	0.427	−0.602
Percent of total variance	64.1%	18.7%	9.6%

Murrelet groups. Significant differences between ground- and tree-nesting populations existed for WING and GAPE. WING measurements were significantly different for all three groups, with Kittlitz's Murrelets having the largest WING and tree-nesting Marbled Murrelets the shortest. The shorter, rounded wings of tree-nesting birds may be associated with nesting in dense old-growth forests while the longer, pointed wings of the other two groups may be adaptations for open habitats like treeless talus slopes where the birds nest. The GAPE of ground-nesting Marbled Murrelet and Kittlitz's Murrelet populations were significantly different from those of tree-nesting Marbled Murrelets but not from each other. This difference is difficult to explain since the other external bill measurements (CULMEN, BDEPEXT) showed no significant differences between the Marbled Murrelet populations, but both were significantly different from Kittlitz's Murrelets. There were no differences in TARS among the three groups.

A PCA of external dimensions showed that specimens of both Marbled Murrelet populations clustered together to form a single cloud of points separate from those of Kittlitz's Murrelets but not from each other (Fig. 3). CULMEN and BDEPEXT had the highest loadings on PC1 and contributed the most to separation of murrelets along this axis (Table 2). PC1 accounted for 64.1% of the total variation. TARS and BDEPEXT had the highest loadings on PC2 which accounted for 18.7% of the total variation. PC3 explained only 9.6% of the variation. WING and TARS had the highest loading on PC3.

There were three trends in the ANOVA's of skeletal dimensions. (1) Both populations of Marbled Murrelets had larger skull measurements (PRL through DIAM) than Kittlitz's Murrelets (Table 3). Kittlitz's Murrelets were significantly smaller than both Marbled Murrelet populations for four of the six skull measurements. There were no significant differences ($P < 0.05$) between ground- and tree-nesting Marbled Murrelets for four of the six skull dimensions (Table 3). BDEP and MANDL dif-

TABLE 3

RESULTS FROM ANOVA OF DIFFERENCES IN SKELETAL DIMENSIONS BETWEEN TREE-NESTING MARBLED MURRELETS, GROUND-NESTING MARBLED MURRELETS AND GROUND-NESTING KITTLITZ'S MURRELETS[a]

Character	Marbled Murrelet (tree)	Marbled Murrelet (ground)	Kittlitz's Murrelet (ground)	Significance
PRL	29.18	29.41	26.22	0.0001
(N, SD)	23, 0.99	27, 1.09	8, 0.75	
SKW	20.11	20.10	19.84	ns
(N, SD)	24, 0.49	29, 050	12, 0.62	
SKL	60.60	61.71	57.55	0.0001
(N, SD)	23, 1.63	29, 1.27	7, 1.46	
BDEP	3.412	4.82	5.061	0.0001
(N, SD)	25, 1.50	29, 0.22	12, 0.28	
MANDL	48.46	49.38	46.56	0.0001
(N, SD)	23, 1.26	28, 1.20	11, 1.24	
DIAM	12.80	12.98	12.27	0.0003
(N, SD)	24, 0.45	21, 0.47	11, 0.30	
CORL	22.83	22.94	23.81	0.0002
(N, SD)	25, 0.64	29, 0.67	12, 0.63	
STERL	74.04	74.61	74.49	ns
(N, SD)	25, 2.05	29, 2.41	12, 1.65	
KEEL	81.53	82.27	83.35	ns
(N, SD)	25, 2.55	29, 3.17	12, 2.86	
KEED	25.64	26.13	27.34	0.0001
(N, SD)	25, 0.84	29, 0.84	12, 1.20	
SYNMAX	18.25	17.75	18.07	ns
(N, SD)	23, 0.63	27, 0.75	11, 0.76	
FEL	23.45	23.85	23.91	ns
(N, SD)	24, 0.52	29, 0.52	12, 0.87	
TIBL	44.94	45.24	44.44	ns
(N, SD)	25, 1.30	29, 1.20	12, 1.75	
TARL	16.91	17.38	16.95	0.0111
(N, SD)	25, 0.44	29, 0.54	12, 0.92	
HUML	48.84	49.18	50.56	0.0002
(N, SD)	25, 1.05	29, 1.09	11, 1.18	

TABLE 3
CONTINUED

Character	Marbled Murrelet (tree)	Marbled Murrelet (ground)	Kittlitz's Murrelet (ground)	Significance
ULNL	37.18	37.39	41.55	0.0001
(N, SD)	24, 0.94	28, 0.92	12, 1.24	
CARPL	25.51	25.62	27.38	0.0001
(N, SD)	25, 0.74	29, 0.60	12, 0.78	

[a] Means that are underlined are not significantly different from each other according to SNK post hoc comparisons test.

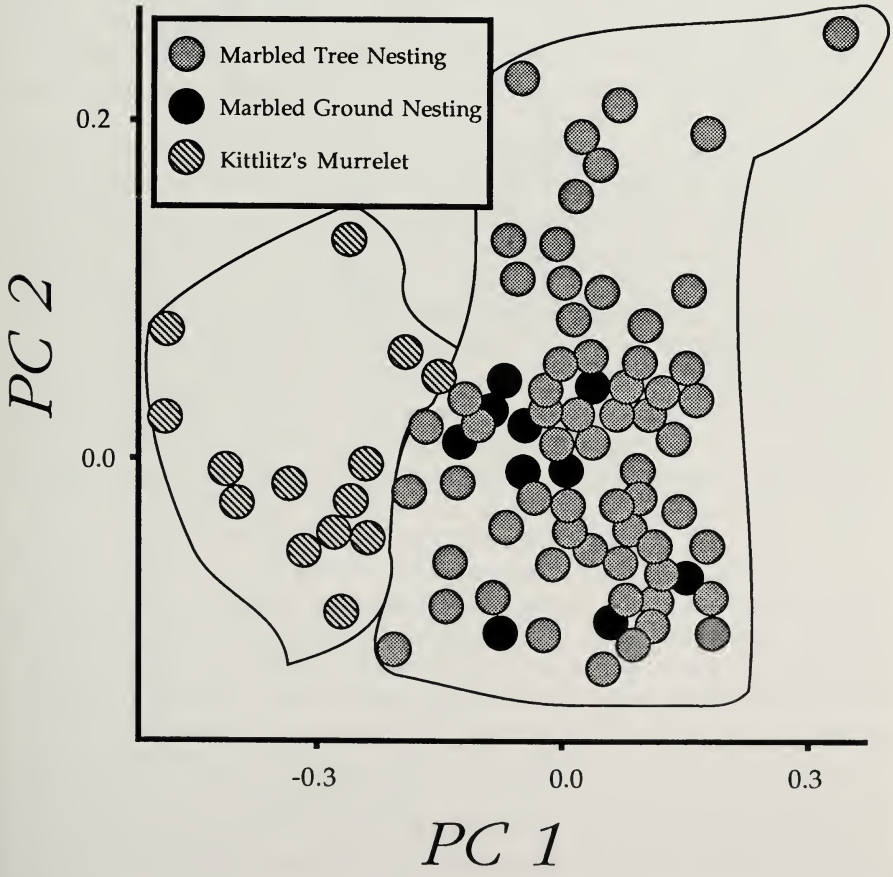

FIG. 3. Plots of PC scores based on external dimensions for each specimen for the first two PC axes.

fered significantly between ground-nesting and tree-nesting Marbled Murrelets ($P < 0.0001$). (2) Kittlitz's Murrelets were significantly larger than all Marbled Murrelets for five of the 11 postcranial dimensions (CORL through CARPL, Table 3). There were no significant differences between ground- and tree-nesting Marbled Murrelets for 10 of 11 postcranial dimensions. (3) TARL, from the hindlimb region, exhibited an interesting pattern of variation. The tree-nesting population was not significantly different from Kittlitz's Murrelets but both were significantly smaller than ground-nesting Marbled Murrelets. It is interesting because it suggests that Kittlitz's Murrelets are more similar to tree-nesting Marbled Murrelets versus ground-nesting Marbled Murrelets for TARL.

Results of the PCA of skeletal measurements were similar to the PCA of external measurements. Plots of specimens along the first two PC axes revealed that Kittlitz's Murrelets occupied a distinct cloud in multivariate space. Ground- and tree-nesting Marbled Murrelets clustered together in a second cloud of points, but they were not segregated from each other (Fig. 4).

The first three PC axes explained 80.3% of the total variance (Table 4). All of the skeletal characters except SKW had positive loadings on PC1. Although SKW's loading is very small compared to the other characters, PC1 should not be regarded as a *size* axis because of the negative loading. ULNL, KEED, and CARPL had the highest loadings on PC1. They contributed the most to the separation of murrelets along the PC1 axis. PC2 and PC3 each had characters with positive and negative loadings indicating that they are shape components. Wing and leg bones contributed most to the separation of specimens along the PC2 axis. TIBL and ULNL had the highest loadings on PC2. PC2 axis explained 17.2% of the total variation. KEEL, TARL, and STERL had the highest loadings on the PC3 axis which accounted for 11.9% of the variation.

We performed several additional analyses (not shown here) using different combinations of skeletal characters. The results of these analyses revealed the same trend as above, separation of Kittlitz's Murrelets from Marbled Murrelets but no separation of ground- and tree-nesting Marbled Murrelets. Analyses (not shown here) of only Marbled Murrelet populations also did not show separation of ground- and tree-nesting populations.

mtDNA analysis.—The Northern Pintail mtDNA probe hybridized well to murrelet DNA, resulting in clear fragment patterns on the autoradiograms (Fig. 5). Murrelet mtDNA contains about 16,000 base pairs. This is similar to other species of birds (Kessler and Avise 1985). Our analysis of five Kittlitz's and 14 Marbled Murrelets shows that each species has distinct mtDNA. All Kittlitz's Murrelets had the same fragment patterns

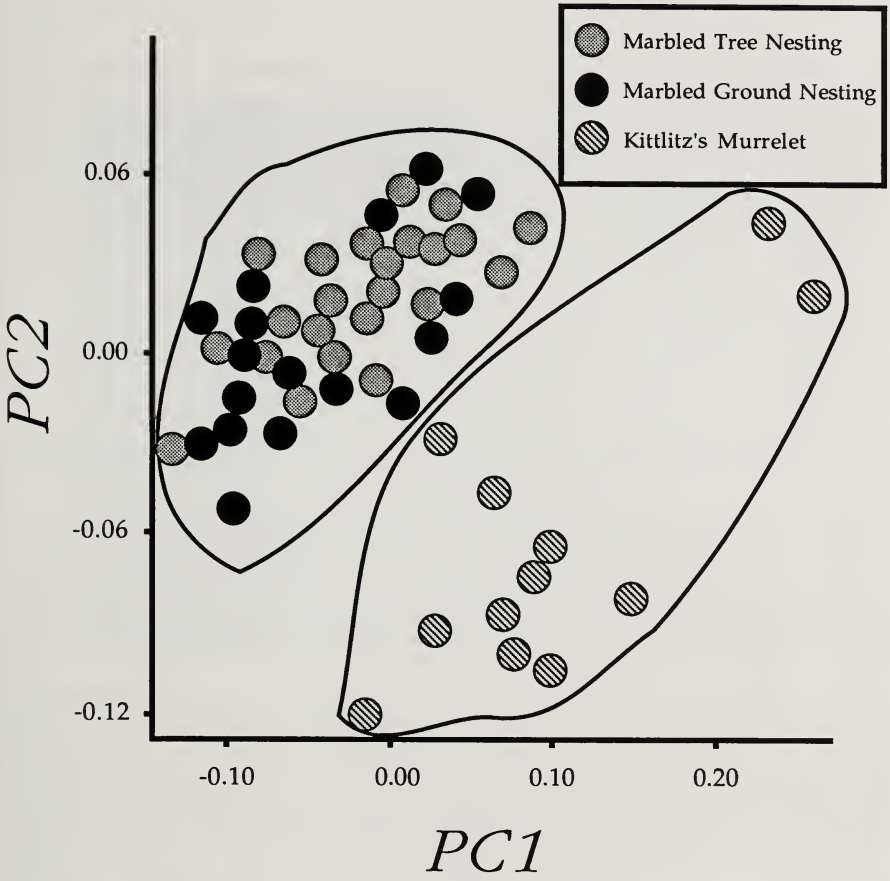

FIG. 4. Plots of PC scores based on skeletal dimensions for each specimen for the first two PC axes.

for nine restriction enzymes and hence one genotype designated K1 (Fig. 5). The Marbled Murrelets had different fragment patterns than Kittlitz's Murrelets for six (*Eco*RI, *Hin*dIII, *Pvu*II, *Sac*I, *Eco*RV, and *Bgl*I) of the restriction enzymes. With one exception, tree-nesting and ground-nesting Marbled Murrelets had identical fragment patterns for all nine enzymes and a mtDNA genotype designated M1 (Fig. 5). The exception is one ground-nesting Marbled Murrelet from the Shumagin Islands which had a variable pattern for *Bcl*I and a genotype designated M2. There were 27 restriction fragments comprising genotype K1, and 20 each in M1 and M2. Eleven fragments were shared between K1 and M1 ($F = 0.468$, $P = 0.044$), 10 fragments shared between K1 and M2 ($F = 0.426$, $P =$

TABLE 4
LOADINGS OF SKELETAL VARIABLES ON THE FIRST THREE PRINCIPAL COMPONENTS

Character	Prin1	Prin2	Prin3
SKW	−0.013	0.092	0.149
CORL	0.316	−0.047	0.197
STERL	0.184	0.317	−0.426
KEEL	0.290	0.300	−0.516
KEED	0.420	−0.001	−0.328
FEL	0.219	0.219	0.030
TIBL	0.169	0.442	0.264
TARL	0.197	0.530	0.499
ULNL	0.560	−0.473	0.116
CARPL	0.417	−0.218	0.219
Percent of total variance	52.1%	17.2%	11.0%

0.050), and 19 fragments shared between M1 and M2 ($F = 0.95$, $P = 0.003$). As expected, mtDNA of Black-legged Kittiwakes was quite divergent from that of Marbled Murrelets ($F = 0.24$, $P = 0.085$) and Kittlitz's Murrelets ($F = 0.25$, $P = 0.085$) compared to differences between *Brachyramphus* populations.

The divergence observed between Marbled and Kittlitz's Murrelet mtDNA is similar to that observed between other congeneric avian species. For example, Shields and Wilson (1987) reported $P = 0.027$ between the White-fronted Goose (*Anser albifrons*) and the Snow Goose (*A. caerulescens*), and $P = 0.061$ between Brant (*Branta bernicla*) and the Canada Goose (*B. canadensis*). Kessler and Avise (1985) reported a mean $F = 0.46$ for 55 interspecific comparisons of avian congeners. This is very similar to our mean $F = 0.447$ for K1 versus M1 and M2. However, the level of mtDNA divergence among congeneric species varies widely, as indicated by the wide range of F values (0.26–0.96) reported by Kessler and Avise (1985).

MtDNA sequence divergence is not, by itself, a reliable indicator of phylogeny or time of divergence of closely related species, and must be considered in light of morphology, natural history, and variation at other genetic loci (Avise et al. 1990, Cronin et al. 1991b). Because mtDNA is maternally inherited and separate from the chromosomal DNA, it gives a limited view of interspecific relationships. Despite the limitations of mtDNA analyses, our data indicate Marbled and Kittlitz's murrelet populations are genetically distinct whether they are sympatric or allopatric. However, little genetic divergence was observed between ground-nesting and tree-nesting Marbled Murrelets. Genotypes of tree- and ground-nest-

FIG. 5. Autoradiogram of Marbled (M) and Kittlitz's (K) murrelet mtDNA digested with the restriction enzyme *Pvu*II, run on 0.8% agarose gel, blotted onto nylon filter, and hybridized to radioactive Northern Pintail mtDNA probe. The lanes labeled B contain mtDNA of Black-legged Kittiwakes and the lane labeled L contains Lambda virus DNA digested with *Hin*dIII. Numbers along the left side of the figure indicate size of DNA fragments in kilobases. Note that all of the Marbled and Kittlitz's murrelets have distinct fragment patterns.

ing Marbled Murrelets were more similar to each other than either was to Kittlitz's Murrelet.

Our analyses of mtDNA agree with current taxonomic treatments of the species we surveyed. As expected, the largest amount of genetic divergence ($P = 0.085$) was observed between Black-legged Kittiwakes and *Brachyramphus* Murrelets. Analyses of mtDNA among *Brachyramphus* Murrelets, Marbled (M1 genotype) and Kittlitz's (K1) murrelets, revealed a genetic divergence of $P = 0.044$. Using Shields and Wilson's (1987) estimated rate of mtDNA divergence of 2% per million years, we estimate a divergence date for Marbled and Kittlitz mtDNA of approximately 2.2 MYBP. However, genetic divergence between ground- and tree-nesting Marbled Murrelet populations was minimal ($P = 0.00$–0.003). These results are consistent with similar intraspecific comparisons

between populations of *Ammodramus* sparrows ($P = 0.006$, Zink and Avise 1990) or Brown Towhees ($P = 0.001$, Zink and Dittman 1991).

Marbled Murrelets have evolved two vastly different breeding strategies: tree- and ground-nesting. Exploitation of new niches is often accompanied by morphological and genetic divergence. However, we observed little variation between tree- and ground-nesting populations of Marbled Murrelets for mensural and genetic characters. Only five of 23 measurements differed between tree- and ground-nesting Marbled Murrelets. Especially significant is the lack of divergence in leg measurements of ground- and tree-nesting Marbled Murrelets. Terrestrial species show marked divergence in skeletal elements of the hindlimbs when compared to their arboreal congeners (Berger 1952). Furthermore, the Marbled Murrelet is different from all other alcids in having an exceptionally short tibiotarsus and tarsometatarsus—presumably an adaptation for its arboreal nesting habits (Storer 1945). In our comparisons, TARS, FEL, and TIBL were not significantly different among the three murrelet groups (Tables 1, 3). The mean TARL of ground-nesting Kittlitz's Murrelets was closer to that of the tree-nesting Marbled Murrelet than to TARL of the ground-nesting Marbled Murrelet (Table 3). These results seem surprising considering that our data suggest that the ground-nesting Kittlitz's Murrelet may have diverged from the Marbled Murrelet 2 MYA, providing ample time for divergence among Marbled Murrelets to occur. Conservative variation in these characters may be related to adaptations to a marine environment where birds spend most of their time. Divergence between ground- and tree-nesting Marbled Murrelets may yet occur if isolation caused by different nesting behaviors prevents gene flow between them.

Although our sample sizes were small, a concordant pattern has emerged from three different data sets, external measurements, skeletal dimensions, and mtDNA. Ground-nesting and tree-nesting populations of Marbled Murrelets have evolved different breeding behaviors, but this behavioral divergence has not been accompanied by extreme morphological or genetic divergence. Our data suggest that these populations probably comprise the same genetic stock. However, larger sample sizes, analyses of populations from throughout the breeding range, and additional genes are needed to better characterize genetic structure of this species.

ACKNOWLEDGMENTS

This project was funded in part by a Frank M. Chapman Award from the American Museum of Natural History and Institutional Funding from the Kutztown University Research Committee. This manuscript benefited from the constructive comments of Barry Wicklow, Jim Rising, Dan Roby, and an anonymous reviewer. The Alaska Maritime National Wildlife Refuge and the M/V Tiglax provided logistical support for much of the field work. We thank the crew of the M/V Tiglax: Captain Al Bayer, Greg Snedgen, John Jameison,

Eric Nelson, Marcia Maccone, and especially Kevin Bell for their contributions. We also thank Cal Lensink and Kathy Kuletz for use of their facilities during field work in Kachemak Bay and Prince William Sound, respectively.

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Wilson Bull., 107(2), 1995, pp. 251–257

SHEEP CARCASS AVAILABILITY AND USE BY BALD EAGLES

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Abstract.—We studied sheep carcass availability and use by Bald Eagle (*Haliaeetus leucocephalus*) in the Willamette Valley, Oregon, during winter 1990. We determined availability of sheep carcasses every 2–4 days along a 65-km transect. Bald Eagle numbers were counted weekly at five communal roosts. Counts ranged from 13 to 49; immatures consistently outnumbered adults. We calculated persistence rates of 137 sheep carcasses; those <200 m from a road or house were rarely used by eagles and persisted longer than carcasses farther away. Eagles were feeding on sheep carcasses in 83% of feeding observations along the transect, and 87% of 234 Bald Eagle castings contained wool. However, we found no evidence of eagle predation on sheep. Availability of sheep carcasses appears to be a primary factor influencing eagle use of the valley in winter. Our estimate of available sheep carrion/day was more than sufficient to meet the needs of the eagles wintering in the valley. However, if eagle numbers continue to increase or if carrion becomes less available, eagles may leave the valley. We recommend that ranchers make carcasses available to eagles away from sources of human disturbance, rather than burying them as is currently practiced. *Received 6 Aug. 1994, accepted 16 Dec. 1994.*

Bald Eagle (*Haliaeetus leucocephalus*) winter concentrations and communal roosts occur in areas where food is abundant. Concentrations have occurred in response to local fish runs (McClelland et al. 1982, Knight and Knight 1983), waterfowl (Isaacs and Anthony 1987), and large mammal carrion (Hancock 1964, DellaSala et al. 1989). Large mammal carrion scavenged by Bald Eagles often includes domestic livestock (Hancock 1964, Isaacs and Anthony 1987, DellaSala et al. 1989) and may be interpreted by ranchers as predation (O'Gara 1982). In the Willamette Valley of western Oregon, private landowners have reported Bald Eagle depredations on sheep, and at least six Bald Eagles have been reported shot or poisoned within the area since 1986 (G. Anderson, pers. commun.). Based on foraging observations and 45 castings, DellaSala et al. (1989) concluded that winter use of the Willamette Valley by Bald Eagles was related to the availability of sheep carrion and afterbirth. However, DellaSala et al. (1989) did not estimate carcass availability or attempt to determine if predation on lambs occurs. Our objectives were to determine the extent of Bald Eagle consumption of sheep carrion, the availability of carcasses in the valley, and if predation on lambs occurs.

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STUDY AREA AND METHODS

We conducted this study in the southern portion of the Willamette Valley between Eugene and Corvallis, Oregon, next to the foothills of the Cascade Mountains. Elevations on the valley floor range from 60 to 125 m, and prominent buttes rise 100–300 m higher. Annual precipitation (mostly rain) is about 90 cm, and temperatures during this study averaged 20°C (range = −31–41°C). Snow was infrequent, and snow cover never persisted for >two days during the study. The Willamette Valley has been largely converted to agricultural use; fields are bordered by black cottonwood (*Populus trichocarpa*), Oregon white oak (*Quercus garryana*), incense cedar (*Libocedrus decurrens*), and low-growing shrubs along fencerows. Primary land use in the valley is grass-seed production; grass fields provide abundant winter pastures for domestic sheep. Land use in the Cascade Mountains and the Coast Range is primarily for wood products.

We counted Bald Eagles at five communal roosts once each week from 16 January to 4 April 1990. All known roosts were counted simultaneously. Most counts began >2 h before sunset PST and ended at dark. We added the number of eagles present at the roosts when observations began to the number entering roosts to obtain a total. Bald Eagles were considered adults if their heads and tails were mostly white; all others were considered immatures unless age could not be determined.

We determined Bald Eagle food habits from castings collected at roost sites. Castings were analyzed to identify food items; prey were identified to species when possible and were expressed as percent occurrence (Marti 1987). We drove a 65-km line transect (Andersen et al. 1985) to gather data on distribution and abundance of Bald Eagles and sheep carrion. The location of the transect was chosen so that it ran parallel to and within easy flying distance of the five roosts. The maximum distance of any roost to the transect was 15 km, whereas eagles were observed feeding up to 24 km from the roosts. One or two observers searched for sheep carcasses and eagles by driving the route at about 40 km/h between 08:30 and 14:00 h PST every other day (15 Jan–14 Feb) or every third or fourth day (15 Feb–25 Apr). We alternated survey direction of the route. Our ability to detect carcasses differed for sheep with and without eagles feeding on them; therefore, we did not attempt to determine carcass densities. Thus, our estimates of carcass availability represent a minimum of sheep available within the study area. Sheep carcasses were assigned a number, each carcass position was mapped, and the condition was classified as intact, open, or hide and bones. We recorded the age of each sheep carcass (lamb, yearling, adult), number and species of birds present, and distance (m) to a road or house. On subsequent visits to carcasses, we noted use and changes in carcass condition until only hide and bones remained or the carcass had been removed. If we did not know the actual day a carcass was removed or when edible portions no longer remained, we considered that day to be the midpoint between visits. Dead lambs were examined for evidence of predation and were necropsied when necessary to determine if they had been killed by eagles. Lamb carcasses with evidence of subcutaneous hemorrhaging and internal bleeding at the site of puncture wounds along the back were assumed to be eagle kills (Wade and Bowns 1983).

We calculated carcass persistence rates (the daily probability that a carcass would remain in the field after detection) using the Kaplan-Meier survival estimation procedure (Kaplan and Meier 1958) modified for a staggered entry design (Pollock et al. 1989). Carcasses removed from the field were censored. Carcass persistence functions were compared for carcasses ≤200 and >200 m from a road or house using the log rank procedure described by Pollock et al. (1989). We used analysis of variance to test for differences in detection distance for carcasses with and without birds on them.

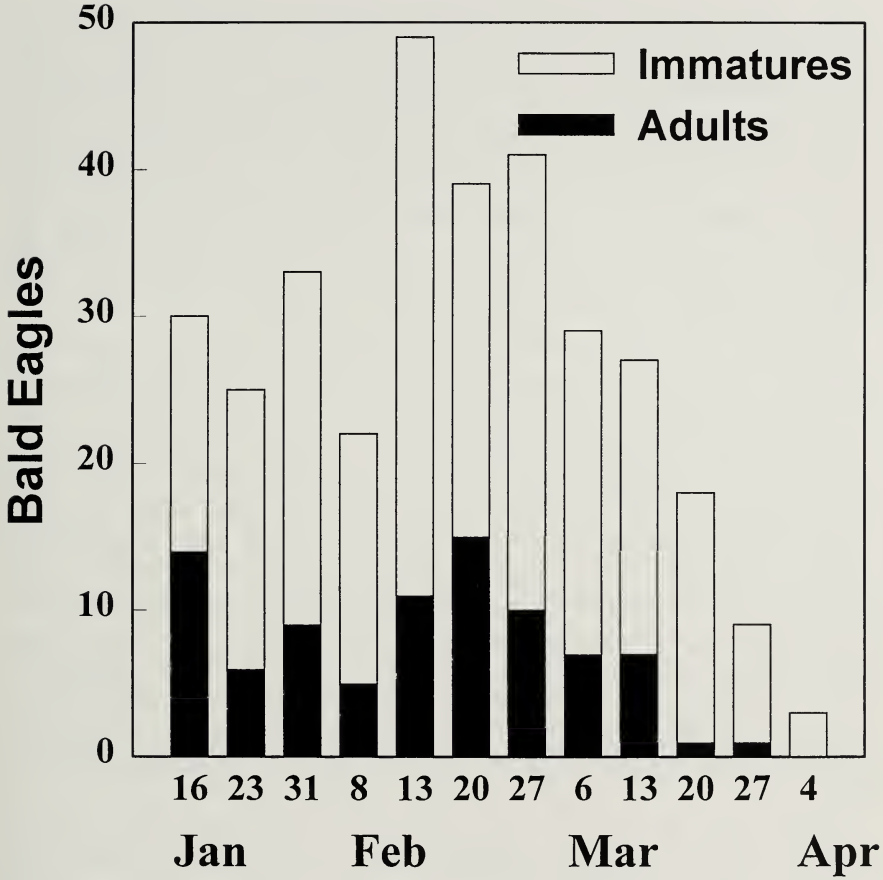

FIG. 1. Number of Bald Eagles observed at communal roosts in the Willamette Valley, Oregon, by date and age class, 1990.

RESULTS

We recorded 339 Bald Eagle sightings (240 immatures, 86 adults, 13 unknown) at five roosts between 16 January and 4 April 1990; the highest count (49) was on 13 February (Fig. 1). Immatures consistently outnumbered adults and remained in the valley longer than adults. We observed eagles feeding along the transect 203 times. Sheep carrion was being eaten in 83% of these observations, and eagles showed no preference for carcasses of lambs over carcasses of older sheep ($\chi^2 = 2.45$, df = 1, $P = 0.13$). We examined 21 lamb carcasses (including seven carcasses that were not found along the transect) on which eagles had fed and five on

which eagles had not fed. We found no evidence of subcutaneous hemorrhaging and internal bleeding, indicating that predators had not killed any of these lambs. We saw no predation attempts on lambs in >200 h observing eagles. The proportion of Bald Eagles eating sheep carrion was similar for immatures (84%) and adults (82%). Of 234 Bald Eagle castings found at communal roost sites, 87% contained wool; no other food item was found in >2.1% of the pellets. Other food items included microtine rodents, nutria (*Myocastor coypus*), brush rabbits (*Sylvilagus bachmani*), ground squirrels (*Spermophilus* sp.), black-tailed deer (*Odocoileus hemionus*), coyote (*Canis latrans*), and cattle.

We found 137 sheep carcasses (19 lambs, 100 yearlings, 14 adults, 4 unknown); we located 38 carcasses on our first transect run and a mean of 3.9 new carcasses/visit thereafter. Forty-six carcasses were removed from the fields by ranchers. A mean of 25.4 carcasses with edible portions remaining were available each day. Carcasses of adult and yearling sheep were from 3 to 1440 m from the road. Carcasses with eagles on them were detected farther away ($\bar{x}$ = 447 m, SD = 392) than those without eagles ($\bar{x}$ = 220 m; SD = 239; F = 14.6; df = 1,111; P = 0.0002). Lamb carcasses were found from five to 405 m away from the road, and those with eagles on them were farther away ($\bar{x}$ = 316 m, SD = 121) than those without birds on them ($\bar{x}$ = 108 m; SD = 102; F = 19.5; df = 1,18; P = 0.0002). Based on descriptions from local sheep ranchers, we estimated that the average adult or yearling sheep weighed about 32 kg, and that about 40% (by weight) of a carcass could be consumed by scavengers.

Carcass persistence rates varied depending upon the location of the carcasses. Eagles used 45 (41.3%) of 109 carcasses that had edible flesh on them when found. Carcasses ≤200 m from a road or house persisted longer than carcasses >200 m away (χ^2 = 25.39, df = 1, P < 0.001) (Fig. 2). About 54% of 137 sheep carcasses were considered accessible to eagles (>200 m from roads or houses); all of these carcasses had edible flesh on them, and 51% were used by eagles. Carcasses rarely persisted > six days before being completely consumed.

DISCUSSION

We believe that the abundance of sheep carrion in 1990 was the primary factor influencing the total number of Bald Eagles wintering in the Willamette Valley. Based on average weight and average number of carcasses, there was a total of about 325 kg of sheep carrion available along the transect/day. We estimated about 155 kg of sheep carrion was accessible to eagles and another 170 kg was present but unlikely to be used by eagles because of its proximity to roads and human habitation or be-

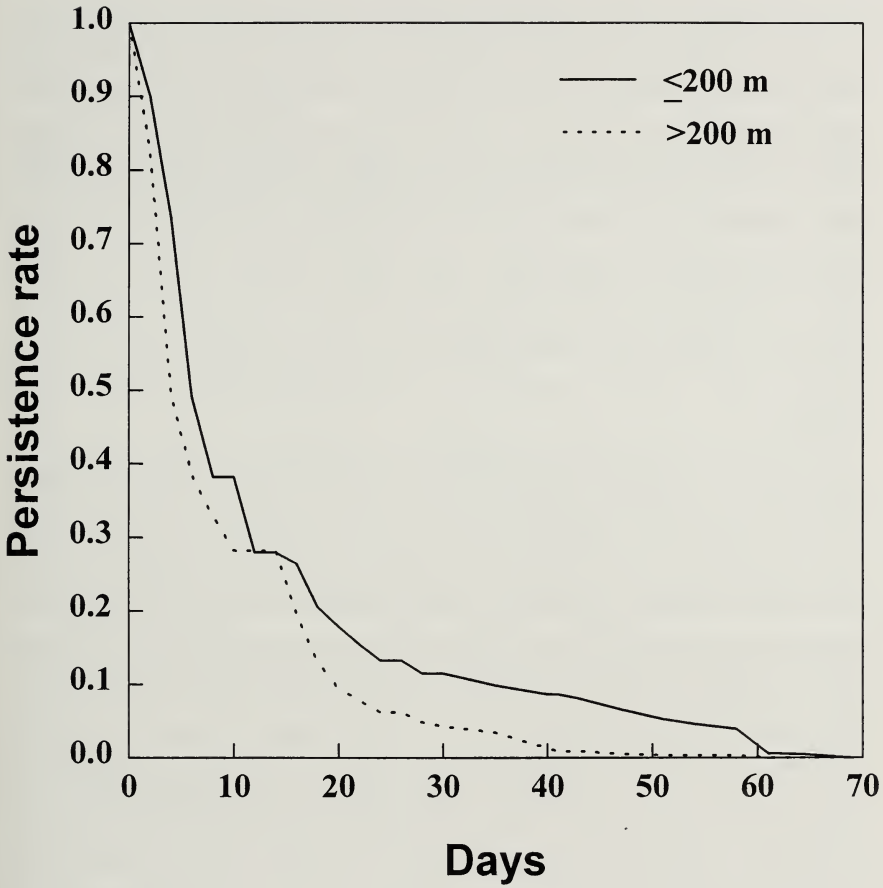

FIG. 2. Sheep carcass persistence rates (the daily probability that a carcass would remain in the field after detection) during winter in the Willamette Valley, Oregon, by distance from roads or houses.

cause the carcasses were intact. Stalmaster and Gessaman (1984) determined that a captive 4.5-kg Bald Eagle requires about 0.3 kg of rabbit/day, and free-ranging eagles require 0.7 kg/day, when the ambient temperature is 20°C. We counted an average of 28 eagles/coordinated roost count, which would require a total of about 20 kg/day of carrion. Thus, our estimate of available carrion/day was more than enough to meet the needs of the eagles in the area. Other scavengers, especially Common Ravens (*Corvus corax*) and coyotes, compete for carrion but are likely accommodated by the carrion surplus to eagle needs.

Based on our 203 foraging-eagle observations and our examination of

26 lamb carcasses, Bald Eagle predation on live lambs was not documented in 1990. Bald Eagle predation on domestic livestock has been suspected in a number of cases (Herrick 1924, Wiley and Bolen 1971, Phillips and Blom 1988) and observed twice (McEneaney and Jenkins 1983). Under most circumstances, it seems that Bald Eagles scavenge rather than prey on livestock. However, O'Gara (1978) noted that Golden Eagle (*Aquila chrysaetos*) predation on sheep increased during periods of decreased natural prey abundance; the observed cases of Bald Eagle predation on sheep by McEneaney and Jenkins (1983) occurred during a winter of abnormally low mortality of mule deer (*Odocoileus hemionus*). Predation on sheep in the Willamette Valley by wintering Bald Eagles is unlikely while carcasses provide an abundant and easily obtained food resource.

Management of carrion to enhance or supplement food supplies for threatened and endangered species is becoming more common. Carcasses have been provided in reintroduction efforts for California Condors (*Gymnogyps californianus* (Wilbur 1978, U.S. Fish and Wildlife Service 1984: 66)). Enhancing or increasing food supplies for Bald Eagles may increase the number of eagles wintering in the Willamette Valley and potentially increase over-winter survival of both adults and immatures (U.S. Fish and Wildlife Service 1986:47). Additional sheep carrion could be made available to eagles by moving carcasses away from roads or houses, not burying carcasses as is often done by ranchers. Sheep carcasses could be scattered in areas away from lambing pastures to minimize conflicts between sheep growers and eagles. This would require wildlife agencies or conservation organizations contacting and educating sheep growers concerning the importance of sheep carrion to eagles. While making these contacts, biologists could inform the growers about the unlikelihood of eagle predation on sheep and teach them to differentiate between predation and scavenging.

ACKNOWLEDGMENTS

The Bureau of Land Management, Eugene District, and the Oregon Department of Fish and Wildlife, Nongame Division, provided funding. Diamond K Ranch, Roseboro Lumber Company, Parker Farms, G. Jelden, and L. Sperlin allowed us access to their property. R. Goggans, L. Poole, D. Wag, Mrs. Ray Valburg, and several volunteers participated in field work. A. Kampfer, L. Kampfer, M. Hanson, C. Bruce, C. Thomas, J. Hackbarth, and J. Thompson provided input and assistance. S. Olson-Edge, B. R. McClelland, and T. G. Grubb provided comments on the manuscript. This is manuscript 10,330 of the Oregon Agricultural Experiment Station.

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Wilson Bull., 107(2), 1995, pp. 258–274

FOOD HABITS OF BALD EAGLES BREEDING IN THE ARIZONA DESERT

Teryl G. Grubb

Abstract.—Of 1814 foraging attempts, prey captures, or nest deliveries by Bald Eagles (*Haliaeetus leucocephalus*) in 14 Arizona breeding areas during 1983–1985, 1471 observations were identifiable to at least class: fish (76%), mammal (18%), bird (4%), and reptile/amphibian (2%). Forty-five species were recorded: catfish (*Ictalurus punctatus, Pylodictis olivaris*), suckers (*Catostomus insignis, C. clarki*), and carp (*Cyprinus carpio*) were most common. Mean population dietary heterogeneity was 2.03 (SD = 0.43). During 1983–1985, 22 successful sites had a wider dietary breadth than nine unsuccessful ones (3.73 vs 1.92). Fish and mammal classes varied by month ($P < 0.001$) and breeding area ($P < 0.001$) and were negatively correlated ($R = -0.993$, $P = 0.001$). Of 484 discrete foraging locations, only four (<1%) were frequented in more than one year. Within-season shifts in foraging locations were typical within breeding areas to accommodate changing prey availability. Foraging activity varied hourly and among prey classes, peaking 08:00–10:00 and 16:00–19:00 h MST ($P < 0.001$). Perches east (NE-E-SE) of foraging sites were used more often before 13:00 h MST (59.3%, N = 118), while perches west (SW-W-NW) were used more often after 13:00 h (58.4%, N = 113; $P = 0.013$). Most foraging occurred near shore in shallow river waters. The mean straight-line distance between Verde River nest sites was 14.4 km (SD = 3.5) with a ratio of river : straight-line distance of 1.4:1. Opportunistic and breeding area-specific foraging was evident throughout the population. *Received 2 May 1994, accepted 11 Nov. 1994.*

Bald Eagles (*Haliaeetus leucocephalus*) typically nest along marine coastlines and large interior lakes and rivers where they have evolved as a fish-eating sea eagle. Food habits have been studied extensively throughout the Bald Eagle's range (Grubb and Hensel 1978, McEwan and Hirth 1980, Cash et al. 1985, Brown et al. 1991); their opportunistic foraging habits are well known (Brown and Amadon 1968). Hunt et al. (1992) summarized the progressive accumulation of food habits data in Arizona through the mostly unpublished research of Rubink and Podborny (1976), Hildebrandt (1981), Haywood and Ohmart (1986) and Grubb (unpubl. data). The purpose of this paper is to document more fully the food habits results of interagency cooperative research led by the USDA Forest Service on Bald Eagles breeding in central Arizona during 1983–1985 (Grubb, unpubl. data), which was an extension and expansion of previous Arizona studies. In this study observations of food habits (foraging attempts, prey captures, nest deliveries), supplemented by prey remains collected from nests, were used to determine dietary composition

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and variability, foraging habits, and foraging habitat for breeding Bald Eagles in central Arizona.

METHODS

The study area in Gila, Maricopa, and Yavapai counties of central Arizona primarily is within the Verde and Salt river drainages, which flow from the north and east of Phoenix, respectively (Fig. 1). This area lies within the transitional Central Highlands Province, characterized by more closely clustered mountain ranges and smaller, less numerous desert basins than the Basin and Range Province to the south, and by generally lower elevation and greater topographic relief than the Colorado Plateau to the north (Chronic 1983). Study area elevations ranged between 500–1500 m, with most Bald Eagle nests (9–11 of 13 during any year) located on 50–100 m cliffs. All sites were associated with riparian vegetation—Cottonwood-Willow (*Populus fremontii-Salix goodingii*) Series and Mixed Broadleaf (*Platanus wrightii, Fraxinus pennsylvanica, Alnus oblongifolia*) Series. However, Sonoran Desertscrub—Arizona Upland or Palo Verde-Mixed Cacti (*Cercidium* spp.-*Opuntia* spp.) Series—was the prevalent vegetative classification. Higher elevation sites ranged into Pinyon-Juniper (*Pinus edulus-Juniperus* spp.) and Ponderosa Pine (*P. ponderosa*) Associations (Brown 1982).

This study was based on more than 51,000 h of field observation by 71 nest watchers deployed near nest sites (Forbis et al. 1985) in 14 Bald Eagle breeding areas in 1983–1985. Species lists were compiled primarily from identifications made during observations (see Forbis et al. for specific techniques) of prey captures and deliveries to the nest. Unquantified prey remains collected at nests during the banding of 6–8-week-old eaglets were used to augment observational species lists. Comparisons among years, months, and breeding areas were facilitated by simultaneous sample days of data collection standardized across all breeding areas (4 days/2 weeks, 20–24 sample days/area/year, i.e., late incubation through fledging, February/March through early June). Each sample day consisted of dawn-to-dusk observation by two nest watchers typically stationed 300–500 m from and with good views of the nest and surrounding foraging/perching habitat.

Locations of foraging attempts and captures were recorded with the Universal Transverse Mercator (UTM) planar coordinate system. Repetitive use of foraging locations was evaluated with both exact (≤20-m accuracy) and truncated (100-m block) UTMs (Grubb and Eakle 1988). Observation times were recorded exactly, but data were partitioned into 15 hour classes for temporal analysis: <06:00, 06:00–06:59 . . . 18:00–18:59, ≥19:00 h MST. Size of fish prey (<15, 15–30, 31–45, >45 cm) was estimated from comparison with adult features or reference points of known dimension at the nests. Species identification and occasional recovery of dropped prey items also facilitated size estimation. Hunting and capture methods, characteristics of foraging perches (type, direction, and distance from foraging area and height above), activity at initiation of foraging attempts/captures, type of foraging habitat (river/reservoir/upland, proximity to shore, and estimated depth) and flight direction of prey deliveries also were recorded whenever possible. Most measurements were recorded indirectly from topographic maps.

Straight-line and river distances were measured between five traditional and three new nest sites on the Verde River to evaluate the amount of riverine habitat required for Bald Eagle breeding areas in central Arizona. For this analysis, nest sites were arbitrarily assumed to be at the center of linear, riverine breeding areas. The Verde River was used because in contrast to the Salt River, (a) it is free flowing over most of its length; (b) it has only two reservoirs at its lower end, one of which is typically little more than a river channel; (c) it has no major or extensive canyons along its course; (d) all of its breeding areas are located

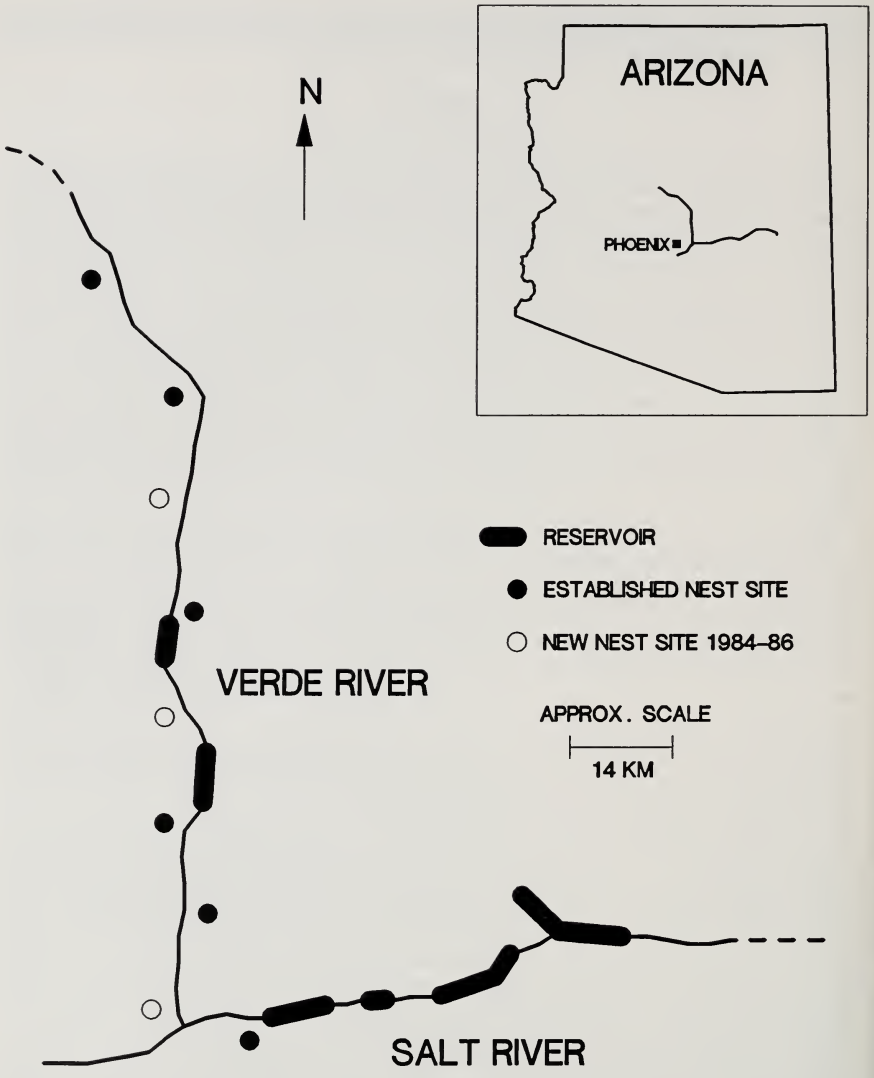


FIG. 1. Central Arizona study area (inset) and spacing of established (pre-1977) and new (1984–1986) Bald Eagle nest sites along the Verde River, as an indication of minimum linear, riverine breeding area size.

along the main river; (e) three new breeding areas were established among five traditional sites during and immediately following this study; and (f) breeding areas were evenly distributed along its course.

Frequency, descriptive, and cross-tabulation programs within SPSS PC+ Version 4.0 (No-

rusis/SPSS Inc. 1990) were used initially to explore and summarize data. Statgraphics Version 5 (STSC, Inc. 1991) was used to compare frequencies among years, breeding areas, prey and size classes (contingency table), and for assessing hourly foraging activity (Chi-square goodness of fit). A nonparametric permutation test (Mielke 1984) enabled comparison of dietary breadth indices between successful and unsuccessful nests. Sample sizes occasionally varied throughout the analyses due to missing data.

Population dietary breadth (PDB), an index to number of prey taxa in the diet, and population dietary heterogeneity (PDH), an index to dietary variation among breeding areas within a given year (Steenhof and Kochert 1988), were used for comparisons within- and between-breeding areas and years. PDB was calculated with the formula, $PDB = [\Sigma(P_i^2)]^{-1}$, where P_i was the proportion of the diet contributed by the *i*th of N prey taxons. Values of this index range from 1 to N. Breadth measures were based on frequencies of individual species when known; otherwise, genus or class groups were used. Calculation of dietary breadth (DB) for individual breeding areas followed the same procedure as PDB. PDH was calculated from contingency tables of prey taxa grouped similarly to PDB for each breeding area. The resultant *G*-statistic (Sokal and Rohlf 1981) was then divided by degrees of freedom, i.e., the product of (prey taxa − 1) × (breeding areas − 1) for the appropriate year.

RESULTS

Prey composition and variability.—Of 1814 food habits observations during 1983–1985, 1471 (81%) were distinguishable to at least class and represented a minimum of 45 separate prey species (Table 1). Fish were the most frequently recorded prey, followed by mammals, with only limited numbers of bird and reptile/amphibian prey evident in the diet. The most common species or groups by prey class were catfish (*Ictalurus punctatus, Pylodictis olivaris*), suckers (*Catostomus insignis, C. clarki*), and carp (*Cyprinus carpio*); cottontail (*Sylvilagus audubonii*), jackrabbit (*Lepus* spp.), squirrel (*Spermophilus* spp.), and woodrat (*Neotoma* spp.); American Coot (*Fulica americana*); other waterfowl (*Anas* spp.); and Sonora mud turtles (*Kinosternon sonoriense*), spiny softshell turtles (*Trionyx spiniferus*), and snakes (Serpentes). Many smaller birds were identified from single occurrences in prey remains. No snake remains were found in nests. Foraging on frogs (Salentia) was observed once, and a partial exoskeleton of a crayfish (*Camberus* sp.) was found in one nest.

Relative frequencies of prey classes in the population diet did not vary significantly across years ($\chi^2 = 3.046$, df = 6, $P = 0.803$); however, the proportions of fish ($\chi^2 = 28.793$, df = 4, $P < 0.001$) and mammals ($\chi^2 = 21.687$, df = 4, $P < 0.001$) in the diet differed from month to month. Bird ($\chi^2 = 4.175$, df = 4, $P = 0.383$) and reptile/amphibian ($\chi^2 = 1.020$, df = 4, $P = 0.907$) variation was negligible (Fig. 2). The relative frequencies of fish and mammal prey were highly and negatively correlated ($R = -0.993$, $P = 0.001$): fish increased in the diet as the nesting season progressed, while occurrence of mammalian prey declined. The proportions of fish ($\chi^2 = 110.586$, df = 11, $P < 0.001$), mammal ($\chi^2 = 128.452$, df = 11, $P < 0.001$), bird ($\chi^2 = 88.197$, df = 11, $P < 0.001$), and reptile/

TABLE 1

FREQUENCY AND RELATIVE PROPORTION (%) OF PREY TAXA IDENTIFIED DURING CAPTURES/DELIVERIES BY BREEDING BALD EAGLES AT 14 ARIZONA NEST SITES, 1983–1985.[a]

Prey taxa	1983	1984	1985	Total
FISH[b]	203 (73)	235 (71)	680 (79)	1118 (76)
Catfish	33	13	75	121
Sucker	13	20	69	102
Carp (*Cyprinus carpio*)	28	28	44	100
Bass	—	3	21	24
Unidentified fish	129	171	471	771
Mammal[c]	56 (20)	65 (19)	142 (16)	263 (18)
Cottontail (*Sylvilagus audubonii*)	13	8	29	50
Black-tailed jackrabbit (*Lepus californicus*)	2	2	3	7
Unidentified lagomorph	0	5	9	14
Squirrel	0	8	10	18
Woodrat (*Neotoma*) spp.	0	7	9	16
Unidentified mammal	41	35	82	158
Birds[d]	11 (4)	24 (7)	24 (3)	59 (4)
Waterfowl	0	10	12	22
Other birds	11	14	12	37
Reptile/amphibian[e]	9 (3)	9 (3)	13 (2)	31 (2)
Turtle spp. (Cryptodira)	6	5	1	12
Snake spp. (Serpentes)	2	6	4	12
Unidentified reptile/amphibian	1	2	4	7
Totals	279	333	859	1471

[a] 343 observations of unknown prey class were excluded; additional species identified from prey remains are listed in footnotes.

[b] Channel catfish (*Ictalurus punctatus*), flathead catfish (*Pylodictis olivaris*), Sonora sucker (*Catostomus insignis*), desert sucker (*C. clarki*), Yellow bass (*Morone mississippiensis*), smallmouth bass (*Micropterus dolomieui*), bass spp. (*Micropterus* spp.), and sunfish spp. (*Lepomis* spp.).

[c] Rock squirrel (*Spermophilus variegatus*), ground squirrel spp. (*Spermophilus*) spp., mouse (*Peromyscus*) spp., muskrat (*Ondatra zibethicus*), ringtail (*Bassariscus astutus*), striped skunk (*Mephitis mephitis*), collared peccary (*Tayassu tajacu*), beaver (*Castor canadensis*), and hereford calf (*Bos taurus*).

[d] Mallard (*Anas platyrhynchos*), Green-winged Teal (*A. crecca*), Cinnamon Teal (*A. cyanoptera*), Common Merganser (*Mergus merganser*), American Coot (*Fulica americana*), White-winged dove (*Zenaida asiatica*), Mourning Dove (*Z. macroura*), Greater Roadrunner (*Geococcyx californicus*), Violet-green Swallow (*Tachycineta thalassina*), Gambel's Quail (*Callipepla gambelii*), Northern Mockingbird (*Mimus polyglottos*), Wild Turkey (*Meleagris gallopavo*), Whip-poor-will (*Caprimulgus vociferus*), Northern Flicker (*Colaptes auratus*), Gila Woodpecker (*Melanerpes uropygialis*), Cactus Wren (*Camplyorynchus brunneicapillus*), Great-tailed Grackle (*Quiscalus mexicanus*), jay spp. (Corvidae), and blackbird spp. (Emberizidae).

[e] Sonora mud turtle (*Kinosternon sonoriense*), spiny softshell turtle (*Trionyx spiniferus*), racer (*Coluber constrictor*), lizard spp. (Sauria), and frog spp. (Salientia).

amphibian ($\chi^2 = 23.411$, df = 11, $P = 0.015$) varied among 12 breeding areas (Fig. 3); two areas with insufficient sample size ($N \leq 8$ observations) were excluded from this analysis.

The range in DB was 2.66–7.51 (ADB) for individual breeding areas across years and 4.88–7.94 (PDB) for years across breeding areas (max-

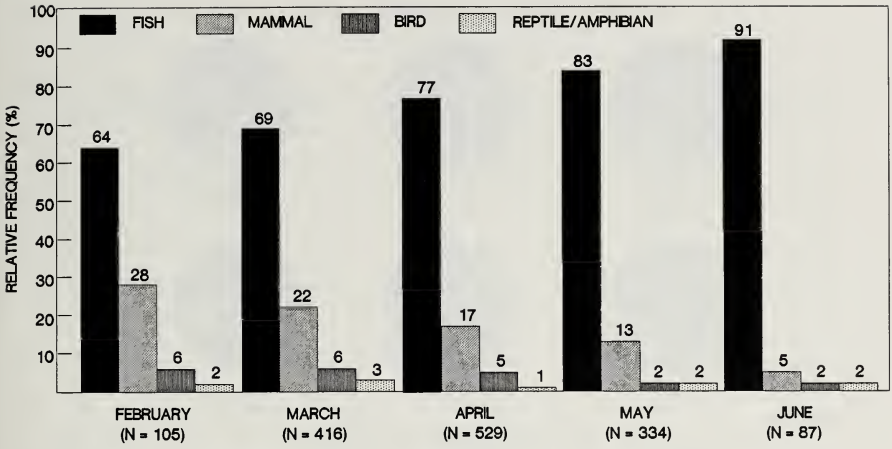


FIG. 2. Monthly variation in relative frequency (%) of breeding Bald Eagle prey classes observed in Arizona, 1983–1985.

imum potential value = 12, Table 2). During 1983–1985, the 22 sites that successfully produced young eagles had a mean DB nearly twice that of nine unsuccessful ones (3.58 vs 1.89; $P = 0.0432$). Mean PDH over the three-year study period was 2.03 (SD = 0.43).

Prey class representation in the diet did not vary significantly between food habits observations and prey remains ($\chi^2 = 3.846$, df = 3, $P = 0.278$). Ten of 11 breeding areas (91%) where both fish foraging was observed and prey remains were collected contained fish remains in or below the nests. Mammals were evident in prey remains at eight of nine breeding areas (89%) with recorded mammal foraging. Bird remains were in seven of nine areas (78%) with recorded avian foraging. In contrast, evidence of reptile/amphibian prey was found only in one of five areas (20%) where such foraging was observed.

Foraging habits.—Over the three-year study period, 484 discrete foraging locations were identified from 743 observations of prey attempts or captures in 14 breeding areas (Table 3). Within the same breeding season, 103 foraging locations (21%) were used more than once (median = 2, range = 2–25). However, only four (<1%) of the 484 locations were frequented in more than one year. Each of the four locations was used only once in either 1983 or 1985, with all repetitive use (range = 2–6) occurring in the alternative year. Using 100-m blocks instead of exact locations in the analysis resulted in 23 (6%) of 363 discrete blocks repetitively used between years. None of the repeat blocks was used all

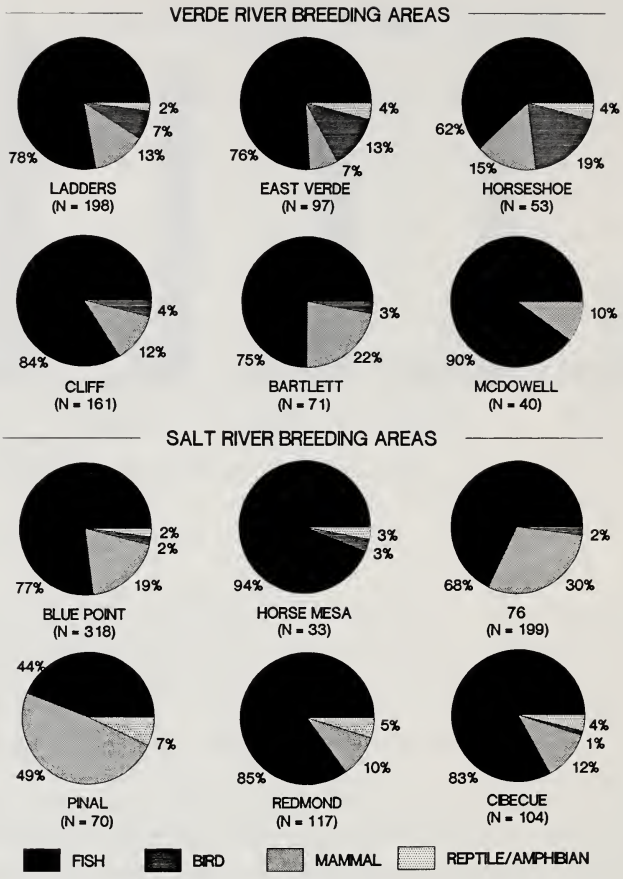


FIG. 3. Variability in the relative frequency (%) of prey classes among 12 Bald Eagle breeding areas in Arizona, 1983–1985.

three years, but 12 were used in consecutive years. Only three blocks had more than one repetition in both years.

The 76 and Blue Point breeding areas illustrate typical between- and within-year variation in foraging patterns. The 76 site had 77% of the 1983 foraging in the northeast quadrant from the nest, 9% northwest, and 14% southwest (N = 22). In 1984 foraging shifted: 25% northeast, 63% northwest, and 12% southwest (N = 16; $\chi^2 = 17.944$, df = 2, $P < 0.001$). At Blue Point in 1983 frequencies for predominant direction of prey delivery flights (east, west, other; N = 83) varied as the season progressed: February and March 52% east, 48% west, 0% other; April 10%, 50%, 40%; May 35%, 0%, 65%; $\chi^2 = 197.396$, df = 6, $P < 0.001$).

TABLE 2

POPULATION (P), AREA (A), AND YEARLY DIETARY BREADTH (DB) AND YEARLY POPULATION DIETARY HETEROGENEITY (PDH) FOR 14 BALD EAGLE BREEDING AREAS IN ARIZONA, 1983–1985

Breeding area	1983 DB	1984 DB	1985 DB	ADB
Ladders	3.69	—	3.05	4.39
East Verde	1.80	6.55	3.33	6.08
Horseshoe	1.00	2.81	4.23	4.36
Bartlett	—	1.00	3.84	4.40
McDowell	—	—	4.08	—
Blue Point	1.00	7.06	6.75	7.51
Horse Mesa	2.00	1.00	2.67	3.76
76	2.57	4.08	3.32	4.11
Sheep	2.00	—	—	—
Pinal	1.92	3.01	—	3.57
Redmond	2.38	2.00	2.86	2.85
Cibecue	—	3.80	5.41	5.19
Cliff	—	3.51	2.14	2.66
Pleasant	—	—	1.00	—
Yearly PDB	4.88	7.94	6.25	
Yearly PDH	2.11	1.57	2.41	

Foraging activity occurred throughout daylight hours (Fig. 4). It increased to a morning peak between 08:00–10:00 h MST, then dropped off to remain relatively steady through midday. A second peak of activity occurred in late afternoon between 16:00–19:00 h MST ($\chi^2 = 198.967$, df = 14, $P < 0.001$). Foraging for both fish ($\chi^2 = 120.514$, df = 14, $P < 0.001$) and mammals ($\chi^2 = 58.294$, df = 14, $P < 0.001$) followed a similar pattern, although mammal foraging showed more of a down-up cycle through midday. Avian foraging fluctuated throughout the day but generally tended to increase toward a peak between 16:00–17:00 h MST ($\chi^2 = 25.250$, df = 13, $P = 0.021$). Reptile/amphibian hourly variation was not significant ($\chi^2 = 14.333$, df = 11, $P = 0.215$); however, a tendency toward increased midday activity is apparent in Fig. 4. No reptile/amphibian predation was observed before 06:00 or after 18:00 h MST.

The distribution of fish size during 1983–1985 was similar to that recorded by Haywood and Ohmart (1986) for 1979–1982. Of 1000 estimated fish prey sizes, 13% were <15 cm; 56%, 15–30 cm; 26%, 31–45 cm; and 4%, >45 cm. Relative frequencies of size varied between Verde (12, 50, 33, 5%; N = 439) and Salt river (15, 61, 21, 3%; N = 454) breeding areas (N = 5 for each river), with higher proportions of fish >30 cm on the Verde River and <31 cm on the Salt River ($\chi^2 = 9.967$,

TABLE 3
FORAGING OBSERVATIONS[a]

Nest	Discrete foraging locations				Locations[b] resused within year	Distrib. of reuse[c]	Locations reused >1 year
	1983	1984	1985	Total			
Ladders	5	9	15	28	9	13, 10, ≤5	0
East Verde	3	6	11	20	2	≤3	0
Horseshoe	4	10	2	16	1	2	0
Cliff	—	13	35	48	14	23, 15, 6, ≤4	1
Bartlett	3	4	22	29	2	2	0
McDowell	—	—	5	5	1	4	—
Blue Point	80	9	74	163	49	25, 7, 6, 6, ≤5	2
Horse Mesa	4	11	9	24	1	2	0
76	15	10	44	69	10	6, ≤4	1
Sheep	2	—	—	2	1	2	—
Pinal	12	6	0	18	1	3	0
Redmond	9	2	24	35	8	6, ≤4	0
Cibecue	—	9	17	26	5	≤3	0
Pleasant	—	1	0	1	0	—	—
Totals	137	89	258	484	103 (21%)	2–25	4 (<1%)

[a] As represented by attempts or captures by year, including the number reused within years, range of repetitive use, and the number used more than one year.
[b] For Ladders, nine of the 28 total foraging locations were used more than once in the same year.
[c] For Ladders, one of nine foraging locations was reused 13 times, another 10 times, and the remaining seven were used ≤ five times.

df = 3, $P = 0.019$). The greater relative frequencies of carp (15–45 cm) at Verde River sites and of bass (primarily yellow bass [*Morone mississippiensis*] <15 cm) at Salt River sites (Fig. 5) probably accounted for most of the size variation between rivers in 1983.

Most hunting forays appeared to be initiated from perches (70%) rather than while in flight (30%, N = 468; $\chi^2 = 16.000$, df = 1, $P < 0.001$). However, flying in to pick up prey was the primary capture technique (76%), followed by landing/walking or wading (19%), and pursuit or pirating (5%, N = 435; $\chi^2 = 85.7273$, df = 2, $P < 0.001$).

Mean number of prey deliveries/day at 11 successful breeding areas on 328 sample days in 1984–1985 was 2.2 (SD = 0.86, N = 729). The ratio of male : female deliveries (N = 152) at three successful sites was 1.9:1, while the ratio of male : female time spent feeding young at those sites was 1:1.8 (15 and 26 min/day, respectively).

Foraging habitat.—Generally, foraging perches were in southerly directions from forage sites (51% SE-S-SW and 78% E-SE-S-SW-W, N = 351; Fig. 6). However, perches east (NE-E-SE) of foraging sites were used more often before 13:00 h MST (59.3%, N = 118), while perches

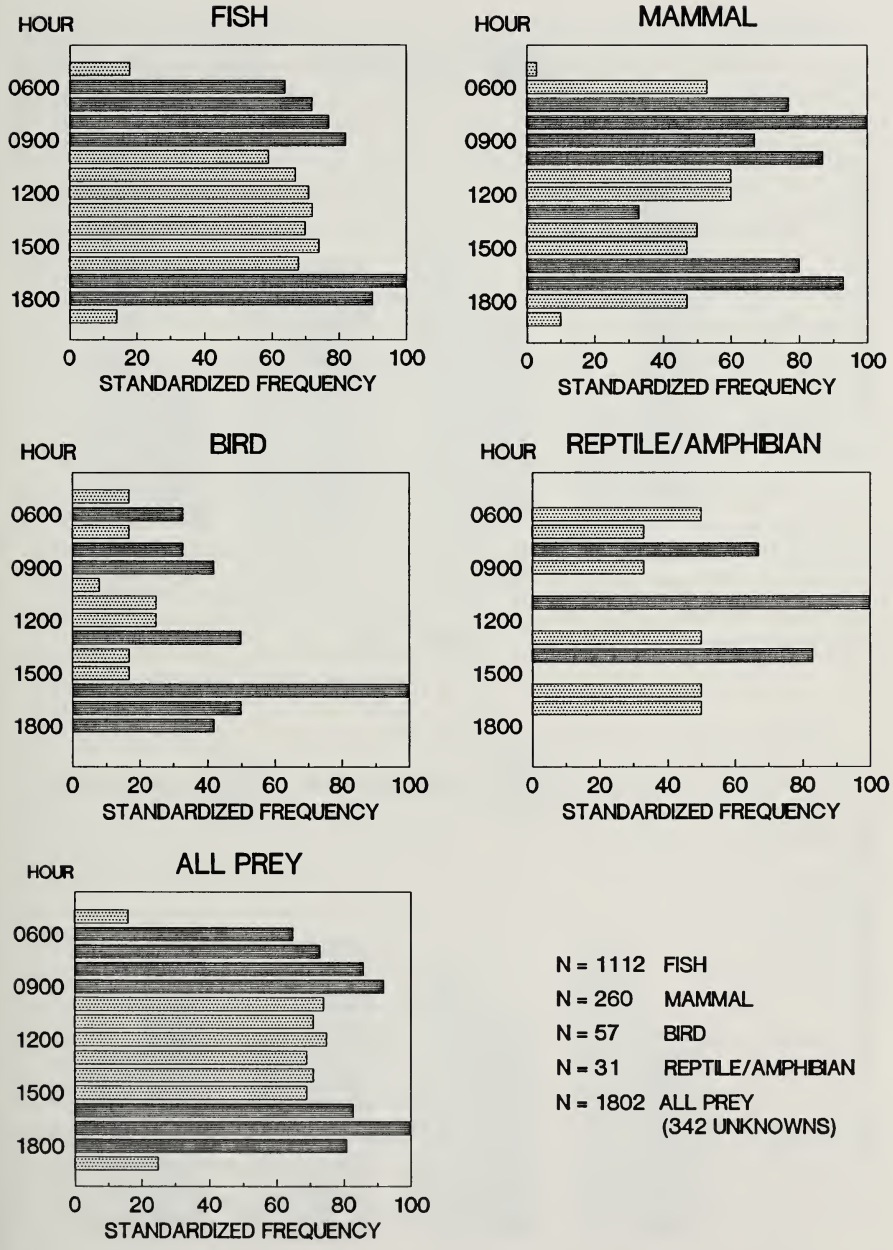
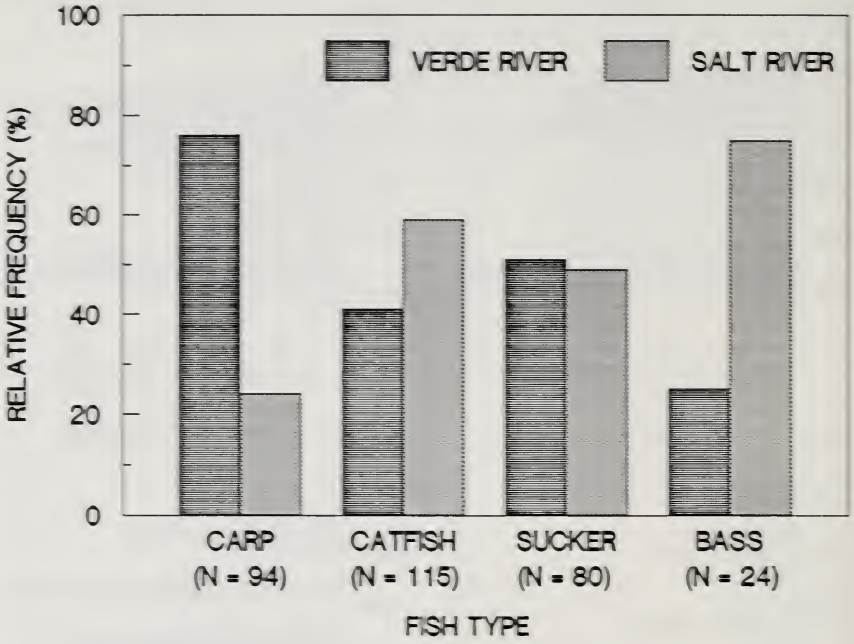
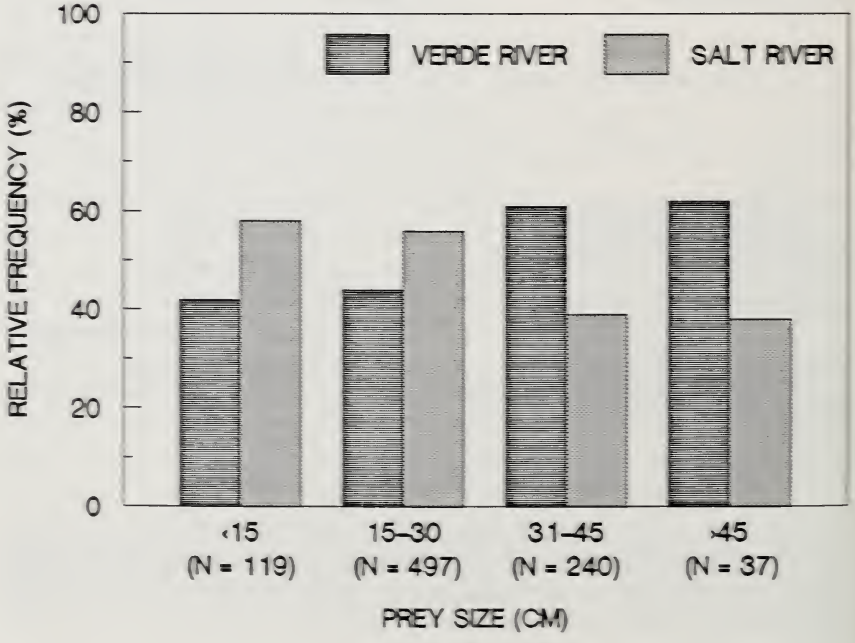


FIG. 4. Temporal patterns of foraging for all prey combined and individual prey classes by breeding Bald Eagles in Arizona, 1983–1985. Frequencies were standardized for comparison by dividing each hourly frequency by the highest frequency in its prey class and multiplying by 100. Shaded bars highlight peaks or trends.


100
80
60
40
20
0
RELATIVE FREQUENCY (%)
VERDE RIVER
SALT RIVER
CARP
(N = 94)
CATFISH
(N = 115)
SUCKER
(N = 80)
BASS
(N = 24)
FISH TYPE


100
80
60
40
20
0
RELATIVE FREQUENCY (%)
VERDE RIVER
SALT RIVER
‹15
(N = 119)
15–30
(N = 497)
31–45
(N = 240)
›45
(N = 37)
PREY SIZE (CM)

west (SW-W-NW) were used more often after 13:00 (58.4%, N = 113; $\chi^2 = 6.162$, df = 1, $P = 0.013$). Foraging perches averaged 22 m in horizontal distance from the foraging sites (SD = 3.1, range 6–73 m, N = 320) and 47 m in vertical height above them (SD = 2.6, range 9–87 m, N = 344). Most foraging perches (60%) were on cliffs, the dominant habitat feature of the study area. Perches in trees (28%: 15% live and 13% dead) and on the ground (12%) were less frequent (N = 367; $\chi^2 = 16.818$, df = 2, $P < 0.001$).

Of 317 water-oriented foraging attempts or captures 20% were along the shoreline, 43% were between shore and the middle third of the water body, and 37% were in the middle ($\chi^2 = 8.636$, df = 2, $P = 0.013$). Sixty-one percent of this foraging occurred at approximate depths of <1.2 m; 20% between 1.2–2.4 m; and 19% deeper than 2.4 m ($\chi^2 = 34.818$, df = 2, $P < 0.001$). River foraging predominated (78%), supplemented by 8% reservoir and 14% upland foraging (N = 465; $\chi^2 = 91.242$, df = 2, $P < 0.001$).

The mean straight-line distance between Verde River nest sites was 14.4 km (SD = 3.5); mean river distance was 18.9 km (SD = 4.8). The ratio of river:straight-line distance was 1.4:1. New sites were located approximately midway in the three longest, straight-line spans (29.0, 26.4, 24.6 km) between established sites (Fig. 1).

DISCUSSION

In support of the observational study of food habits, Mersmann et al. (1992) and Stalmaster and Plettner (1992) found observation to be the least biased means of portraying diets. Todd et al. (1982) and Knight et al. (1990) recommended direct observation to validate prey remains in determining diet because prey remains favored avian over fish classes; this bias was reversed for observed food habits. Despite minor differences noted in their Arizona study, Haywood and Ohmart (1986) felt the two methods were comparable. Collopy (1983) also found no differences ($P > 0.05$) between observation and prey remains in estimating species composition in the diet of golden eagles (*Aquila chrysaetos*) in Idaho.

Prey composition and variability.—Species composition and relative frequency were generally comparable to other breeding Bald Eagle food habits studies in Arizona (see Table 4). Related data on species, size, and number of prey were insufficient for biomass calculations. However, the

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FIG. 5. Comparison of fish prey types and sizes from observations of foraging Bald Eagles along the Verde and Salt rivers in Arizona, 1983–1985.

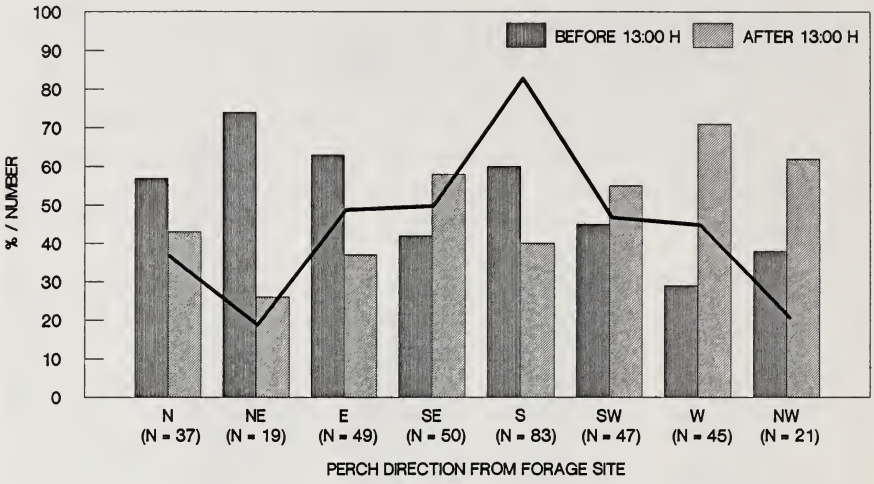

FIG. 6. Breeding Bald Eagle foraging perch directions from foraging sites before and after 13:00 h (relative frequency, bars) and actual perch frequency by direction (line) in Arizona, 1983–1985.

high proportion of mammals recorded in the population diet during this study, along with the unlikelihood of over-estimating mammal frequency in an observation-based study (Stalmaster and Plettner 1992), suggest an unusual dependence on this prey class during 1983–1985. Between 1986–1990, Hunt et al. (1992) noted a higher proportion of birds in the population diet than mammals, yet they found the same seasonal, inverse relationship between primary and secondary prey classes (Fig. 2).

TABLE 4

COMPARISON OF PREY COMPOSITION RESULTS (%) FROM FORAGING STUDIES ON BREEDING BALD EAGLES IN ARIZONA

Study/years		Fish	Mammal	Bird	Reptile	Species	Number of items
Rubink & Podborny (1976)/1972–1975	R[b]	87.3	3.2	6.4	3.2	7	63
Hildebrandt (1981)/1977–1978	R	82.3	9.9	7.2	0.0	20	192
	O	76.2	13.8	10.0	0.0	—	130
Haywood & Ohmart (1986)/1979–1982[a]	R	76.4	12.0	11.0	0.6	30	484
	O	88.0	6.0	1.2	4.8	—	579
Present study/1983–1985[a]	O	76.0	17.9	4.0	2.1	45	1471
Hunt et al. (1992)/1986–1990	R	79.9	7.4	11.8	0.9	72	1847

[a] Based on Grubb (unpubl. data).
[b] R = remains, O = observations.

These inverse relationships between fish and mammals or birds, like those recorded for wintering Bald Eagles in Arizona and New Mexico (Grubb and Kennedy 1982, Grubb 1984), may reflect the opportunistic foraging associated with fluctuating prey and marginal habitat conditions characteristic of the periphery of a species' range. Increased turbidity during spring runoff may have reduced fish availability for eagles early in the nesting season, while improving water conditions with associated spawning likely accounted for the later increase.

Low annual variation in prey composition may have been partially a result of population averages dampening individual variation, and/or the consistent weather and stream-flow patterns during the 1983–1985 nesting seasons. A year of relatively high precipitation, compared with low to average years like those observed during this study, would likely result in greater annual fluctuations of prey use. In contrast to population diet, DB among individual breeding areas from year to year was sufficiently variable to indicate both opportunistic and site-specific foraging activity.

The wider DB of successful sites suggests either a greater reliance on alternate prey or a more diverse variety of prey at those sites. Arizona's breeding Bald Eagles (PDH = 2.03) showed more variation in diet than Prairie Falcons (*Falco mexicanus,* PDH = 1.63), and less than Golden Eagles (PDH = 2.62), and Red-tailed Hawks (*Buteo jamaicencis,* PDH = 2.44) in southwestern Idaho (Steenhof and Kochert 1988).

Foraging habits.—Shifts in foraging location and variable prey composition suggest opportunistic use of habitat for foraging, both within- and between-years. Variation in foraging directions was likely a result of changing water conditions, spawning cycles, and human recreational activity. Different flow rates and turbidity levels in the stream running through the 76 breeding area in 1983 and 1984 may have affected fish prey availability and caused the recorded shift in primary foraging areas. At Blue Point, the April shift to the east corresponded to carp spawning in the adjacent upstream reservoir, whereas the shift back west in May and the increase in off-river flight directions was apparently related to the end of spawning and the seasonal increase in water-oriented human recreational activity.

Hourly foraging results for 1983–1985 generally confirmed previously reported peaks and trends (Haywood and Ohmart 1986) and further supported temporal variability in foraging for all prey classes, including fish. Haywood and Ohmart (1986) identified two peak periods of foraging, 1–4 h and 8–10 h after sunrise (N = 733). Afternoon peaks in 1983–1985 appeared later, but this was probably an artifact of differential time measurement between the two studies. Haywood and Ohmart (1986) also observed a significant difference between individual hours for all prey

classes combined but not for fish alone. Given the variety of prey and range in foraging times recorded during these two studies, it appears that Bald Eagles breeding in Arizona will take most any kind of prey at any time of day as the need and/or opportunity arises.

Feeding rates were within the ranges reported for two nests in Ohio (2.5–4.0 feedings/day, Herrick 1924) and for three nests in southeast Alaska (2.3–3.6 feedings/day, Cain 1985). However, both these studies noted nearly 1:1 ratios of male : female prey deliveries. In Arizona, males appeared to do more prey gathering and less nest attending, although behavior of individual pairs varied. Cain (1985) observed an overall male: female ratio of time spent feeding of 1:1.9, similar to Arizona results, with male participation in feedings declining as the nestling period progressed.

Foraging habitat.—Given the abundance of cliffs throughout the study area and the distribution of riparian vegetation on either side of drainages where it occurred, the availability of potential perching habitat was not directionally biased. Thus, foraging perch use appeared related to position of the sun, with a selection for those sites or times that placed the sun behind the eagle as it viewed the foraging area. Such relative positioning improved visibility above as well as into bodies of water; it also hindered potential prey from detecting the approaching predator (Grubb 1977). In addition, the benefits of shade for thermoregulation at cliff sites may have been a factor in midday perch selection, particularly later in the season when temperatures often rose above 100°F.

Steep, canyon-walled shorelines, and frequent water level fluctuations that limit littoral zones and their ability to support prey species are characteristic of Arizona reservoirs. These factors probably contribute to the predominantly river and upland foraging recorded during this study. Additionally, because most nests were along rivers and observations were usually centered on nest sites, reservoir foraging may have been under represented. Foraging in shallow, near-shore habitat was consistent with the documented importance of shallows and riffles in providing forage for benthic-feeding fish and simultaneously increasing their vulnerability to foraging Bald Eagles (Haywood and Ohmart 1986).

Foraging habitat is one of the primary determinants of raptor breeding area distribution (Newton 1979). The even distribution of breeding areas along the Verde River is strong evidence for a minimum linear, riverine breeding area size for Arizona of approximately 14 km, straight-line distance. The establishment of three new sites midway in each of the three widest gaps between traditional sites further substantiates this trend. Presumably this distribution is driven by prey availability, since Bald Eagles nest much closer together (<0.8 km) in regions of abundant prey (Dzus

and Gerrard 1993). The straight-line river distance ratio of 1:1.4 was calculated on total nest distribution and river distance, yet it compared to the 1:1.5 ratio determined by Grubb (1988) within 3.2 km radii of 18 nest sites. Thus, the indication is that approximately 20 km of riverine habitat may be necessary to support a breeding pair of Bald Eagles in Arizona (14 km straight-line distance × 1.4 straight-line : river distance ratio).

In summary, breeding Bald Eagles in central Arizona opportunistically used a wide variety of prey, although fish, primarily catfish, suckers, and carp, were consistently the most frequent and important prey, especially later in the nesting season. Like wintering Bald Eagles in the Southwest, the breeding population has adapted to variable and ephemeral sources of prey. Consistent with this foraging behavior were within- and between-season shifts in foraging locations and variations in diet among breeding areas.

ACKNOWLEDGMENTS

Field data were collected through the special efforts of 71 USDA Forest Service volunteer nest watchers. W. L. Eakle, J. L. Ganey, and the Institute for Wildlife Studies, Arcata, California (D. K. Garcelon, President) also provided invaluable field and analytical assistance. D. E. Berry facilitated much of the initial, exploratory computer analysis. The original manuscript benefitted from the critical reviews of G. T. Allen, B. T. Brown, M. W. Collopy, and W. S. LaHaye. This paper was derived from research jointly funded by the USDA Forest Service, U.S. Fish & Wildlife Service, and U.S. Bureau of Reclamation.

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Wilson Bull., 107(2), 1995, pp. 275–288

BREEDING BIOLOGY OF SNOWY PLOVERS AT GREAT SALT LAKE, UTAH

PETER W. C. PATON[1]

ABSTRACT.—I studied the breeding behavior of Snowy Plovers (*Charadrius alexandrinus*) in northern Utah from 1990–1993. Nests at Great Salt Lake were initiated over a 14-week period from mid-April to mid-July, and were more comparable to data from California than from Kansas. Breeding males were first resighted from late March through May, whereas females had a more prolonged arrival period from late March through mid-June (N = 256 color-banded adults). Renesting following nest loss was documented only twice, in part because birds often left the study sites. Most females departed immediately after nests hatched, while males exhibited uniparental care of broods. A similar mating system was described for coastal California, where sequential polyandry was documented regularly. During this study double-brooding and sequential polyandry were rarely observed, but both strategies were probably more common than I detected. Mayfield-method estimates of annual nest success ranged from 5.4% to 49.2%, with most nest failures apparently caused by mammalian predators. These results suggest that the breeding strategies of migratory plovers in Utah resemble those of resident and migratory birds nesting in California and Oregon, rather than migratory plovers nesting in the Great Plains. *Received 11 April 1994, accepted 15 Nov. 1994.*

The breeding behavior of Snowy Plovers (*Charadrius alexandrinus*) appears to vary among geographic regions. Warriner et al. (1986) found that plovers nesting in California were double-brooded and sequentially polygamous, while individuals in Kansas were single-brooded and monogamous (Boyd 1972). In coastal California, both sexes shared incubation duties, but males usually exhibited uniparental care of broods once eggs hatched (Warriner et al. 1986). While males remained with broods, females found new mates and initiated second clutches. If young fledged early in the breeding season, males initiated second clutches with new females. In contrast, plovers in Kansas had biparental care of broods (Boyd 1972). A small percentage of European Kentish Plovers (*C. a. alexandrinus*) also exhibit sequential polyandry (Rittinghaus 1956, Székely and Lessells 1993).

Studies of Snowy Plover breeding biology in western North America have focused on populations of Oregon and California (Page et al. 1983, 1985; Wilson-Jacobs and Meslow 1984; Warriner et al. 1986). The most comprehensive study was in coastal California, where many birds in the population were year-round residents (Warriner et al. 1986). Little is known about its breeding biology in the eastern Great Basin, where birds

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are all migratory (Page et al. 1995). There is a need to examine Snowy Plover breeding biology throughout its range because Pacific Coast populations were listed as threatened by the U.S. Fish and Wildlife Service in April 1993 (Federal Register 1993). I report on the migratory and nesting chronology, mating system, and nest success of Snowy Plovers at Great Salt Lake, Utah.

STUDY AREA AND METHODS

I studied Snowy Plovers at two study sites at Great Salt Lake, Davis County, Utah, from 1990 to 1993: Howard Slough Waterfowl Management Area (350 ha; 41°09′N, 112°09′W) and West Layton marsh (400 ha; 41°02′N, 112°05′W). These sites are approximately 10 km apart on the eastern, central shore of the lake. The Utah Division of Wildlife Resources (UDWR) actively manages Howard Slough for waterfowl production using a series of diked impoundments. UDWR personnel controlled mammalian predators at Howard Slough (red fox [*Vulpes vulpes*], striped skunk [*Mephitis mephitis*], and raccoon [*Procyon lotor*]). West Layton marsh (hereafter Layton marsh) is jointly owned and managed by UDWR and the Nature Conservancy, and predators were not controlled at this site. Layton marsh is part of the lake's largest complex of undiked wetlands. Both study sites were dominated by salt flats, interspersed with patches of salt-tolerant plants of the family Chenopodiaceae, including greasewood (*Sarcobatus vermiculatus*), iodine bush (*Allenrolfea occidentalis*), seepweed (*Suaeda* spp.), summer cypress (*Kochia scoparia*), bassia (*Bassia hyssopifolia*), and pickleweed (*Salicornia europaea*). In addition, marsh vegetation increased dramatically over the course of the study and consisted primarily of alkali bulrush (*Scirpus maritimus*), cattail (*Typha* spp.), and phragmites (*Phragmites australis*) (Paton 1994).

From 1990 through 1993, we surveyed study sites at least twice weekly from 15 March through 31 August. Surveys were initiated at Howard Slough on 4 May and at Layton marsh on 13 June in 1990. I worked by myself in 1990 and had one field assistant from 1991 to 1993. We located nests using the nest-searching techniques of Page et al. (1985). Expected hatching dates were determined by floating the eggs (Westerkov 1950) and assuming an egg-laying period of four days and a 27-day incubation period (Warriner et al. 1986, Page et al. 1985). I considered nests successful if at least one chick hatched. Nests were classified as unsuccessful if they were empty prior to expected hatching dates (69.1% of 175 depredated nests), if obvious predator signs were found at nests (18.9%), or if small egg shell fragments (indicating pipping) were absent from the scrape lining after the expected hatching dates (12%). I calculated apparent nest success (i.e., number of successful nests divided by the total number of nests) and Mayfield-method estimates of nest success (i.e., success based on exposure days; Mayfield 1961, Johnson 1979, Johnson and Shaffer 1990). Only nests active for at least one week were used in analyses of clutch size because the egg-laying period can take up to five days (Warriner et al. 1986). Following Page et al. (1983), I defined fledglings as the age class when juveniles were capable of flight. Fledging success was estimated from the mean size of broods at four weeks post-hatching (Page et al. 1983, Warriner et al. 1986).

I captured incubating plovers with a circular funnel trap, or herded them into two mist nets staked together to form a 'V'. Plovers were uniquely marked with four unicolored legbands. We banded 82 adults and 60 immatures (i.e., where immature equals both chicks and fledglings) at the sites in 1990, 142 adults and 22 immatures in 1991, and 137 adults and 79 immatures in 1992.

Nesting chronology was analyzed by pooling data into ten 15–16 day long periods, from

1 April to 31 August (e.g., 1–15 May, 16–31 May). A likelihood ratio chi-square test (G^2) was then used to compare the goodness-of-fit between the two study sites and among years at the same study site. To determine how long individual plovers remained at the study sites, I used only birds resighted in years subsequent to their initial banding year. I divided these data into two groups: (1) definite breeding individuals because they were captured or observed on a nest (nest confirmed) and (2) birds seen at the focal study sites but never associated with a nest (no nest confirmed). I also calculated the number of days birds remained at the study sites following nesting failure or success. This latter analysis included birds banded in the preceding years and their banding year.

To monitor daily movements of foraging color-banded adults away from their active nests, we conducted biweekly transect surveys of both study sites. We plotted observations of color-banded individuals on field maps (1 cm = 100 m); therefore, observations were accurate to within a 50 m radius of the actual location. Nests were mapped using a satellite-based global positioning system. I used a Mann-Whitney test to compare daily movement distances between the sexes. For this comparison, I used only the mean distance individuals moved within a breeding season to reduce pseudo-replication errors associated with multiple observations on the same bird. In all analyses, statistical significance was based on an alpha level equal to 0.05.

RESULTS

Migratory chronology.—Snowy Plovers began arriving in northern Utah in late March, with the earliest sighting on 19 March 1992. The migratory chronology of adult males differed significantly from that of females ($G^2 = 23.9$, 10 df, $P = 0.008$). Breeding males appeared to arrive during two peak periods; there was a large influx of birds from late March to 31 May and a small peak centered on 1–15 July (Fig. 1). In contrast, confirmed breeding females had an extended arrival period from late March to mid-June. Some banded adult males and females were not resighted at the study sites until late July, suggesting they possibly nested elsewhere that year or were simply transients.

Data on fall departure dates were not complete, as many juveniles were still in northern Utah after systematic fieldwork ended on 31 August. Immature plovers tended to congregate in large feeding flocks during August and September, with up to 350 birds observed in some flocks. Adults accounted for 12.8% of observations (N = 619) during systematic surveys after 15 August, whereas even fewer adults were seen during incidental observations in September (i.e., 2.3% of 608 individuals). I know of no October or November Snowy Plover records in Utah, although there is one record of a Snowy Plover on the south shore of Great Salt Lake in mid-December (C. Kneedy, Utah Ornithological Society, unpubl. data).

Nest chronology.—The egg-laying period usually commenced in the second week of April and continued as long as 14 weeks until the third week of July (range = 10 April–18 July; Fig. 2). As would be expected, given typical climatic variation, there was significant annual variation in

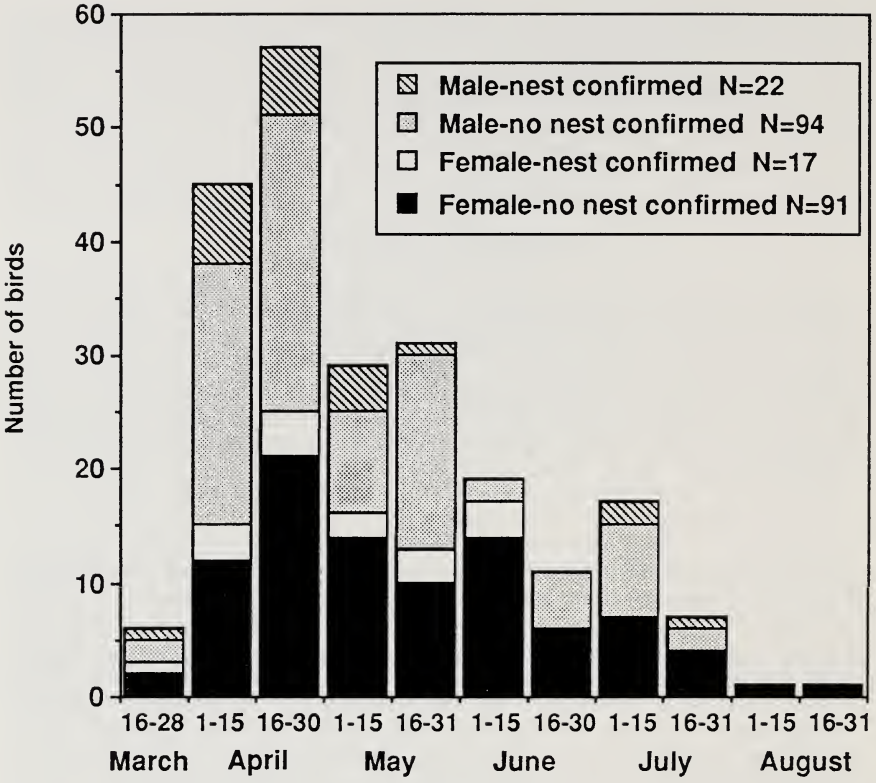

FIG. 1. Arrival dates for confirmed breeding and potentially non-breeding Snowy Plovers (no nest confirmed) at Great Salt Lake.

nest chronology, with the nest initiation chronology differing significantly among years at both Howard Slough (G^2 = 29.1, 14 df, P = 0.01) and Layton marsh (G^2 = 29.7, 14 df, $P < 0.001$). The timing of nest initiations differed between the two sites in 1991 (G^2 = 15.1, 6 df, P = 0.020) and 1992 (G^2 = 19.8, 7 df, P = 0.006) but not in 1993 (G^2 = 7.0, 7 df, P = 0.43).

Breeding adult males had a tendency to be observed for more days than adult females during the breeding season, although this difference was not statistically significant (Mann-Whitney U-test, P = 0.082) (Fig. 3). Breeding female plovers were seen a median of 45 days (25%–75% quartiles = 33–65, maximum = 98 days, N = 17), whereas breeding males were observed a median of 53.5 days (25%–75% quartiles = 39–80, maximum = 149 days, N = 22).

Both sexes left the study sites immediately following nest failure and

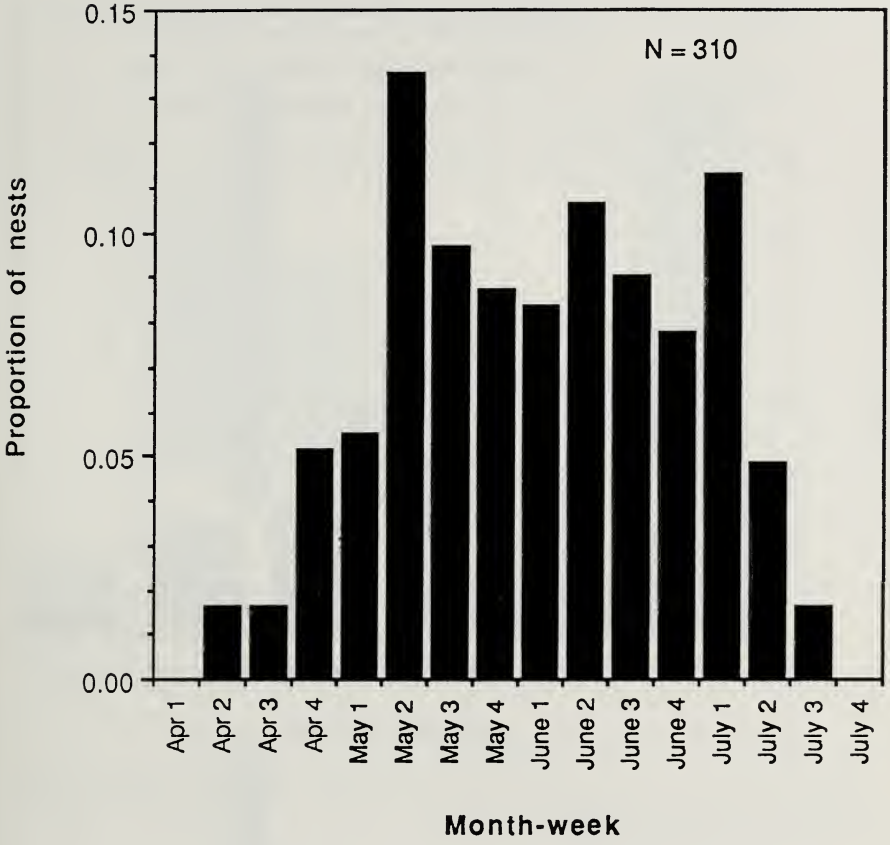

FIG. 2. Nest initiation chronology for Snowy Plovers at Great Salt Lake.

were not subsequently resighted that year (41.5% of 41 females, 46.4% of 28 males; $G^2 = 0.17$, 1 df, $P = 0.68$; Fig. 4). A substantial number of unsuccessful breeding birds were detected for ≥50 days at the same study site (i.e., 29.3% of 41 females and 28.5% of 28 males). However, I only documented the same pair renesting together twice following clutch loss.

Males tended to be detected for longer time periods than females after nests successfully hatched ($G^2 = 17.5$, 4 df, $P = 0.002$) (Fig. 4). The majority of females (57.5% of 47) were not resighted two days after eggs hatched, and only a small percentage of the successful females (16.9% of 47) remained at the study sites for over 25 days. In contrast, most males (63.8%) were observed at the study sites for at least 11 days with their broods. A substantial number of males (23.4%) were not resighted

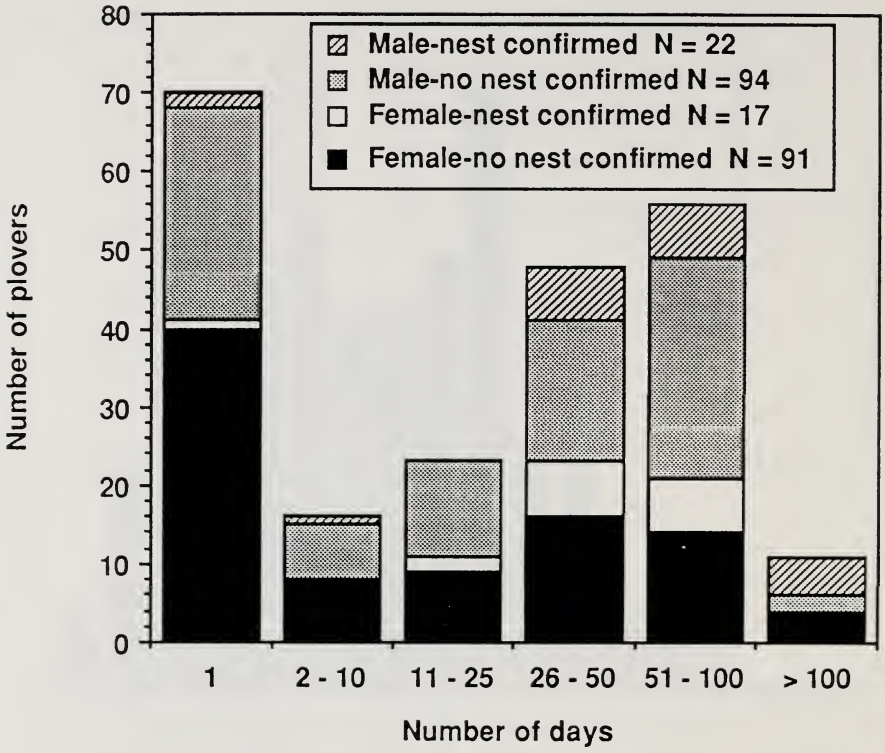

FIG. 3. Number of days that adult Snowy Plovers were detected at study sites during the breeding season. Data are shown by sex for potentially non-breeding birds (no nest confirmed) and breeding birds (nest confirmed).

two days after nests hatched, apparently because they led their broods off the study sites.

Incubation behavior.—Snowy Plovers at Great Salt Lake appeared to defend a relatively small area immediately around the nest (i.e., 10–20 m radius around the nest). Nonincubating parents foraged in areas separate from nest sites, and I rarely observed those birds foraging near nesting areas. Based on observations of color-banded birds known to be associated with active nests, I found that some plovers travelled over 3 km to foraging sites (Fig. 5). Females were found as far as 3770 m from active nests (median = 177 m, 25%–75% quartiles = 64–466 m, N = 192

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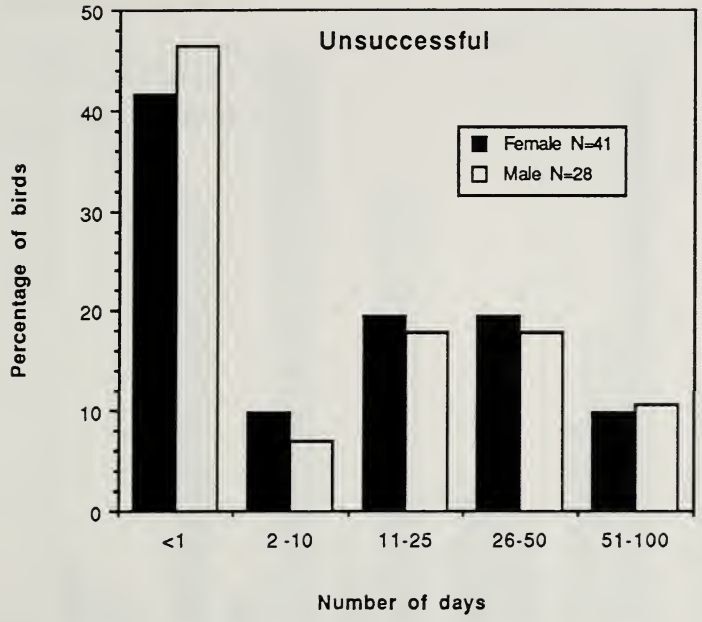
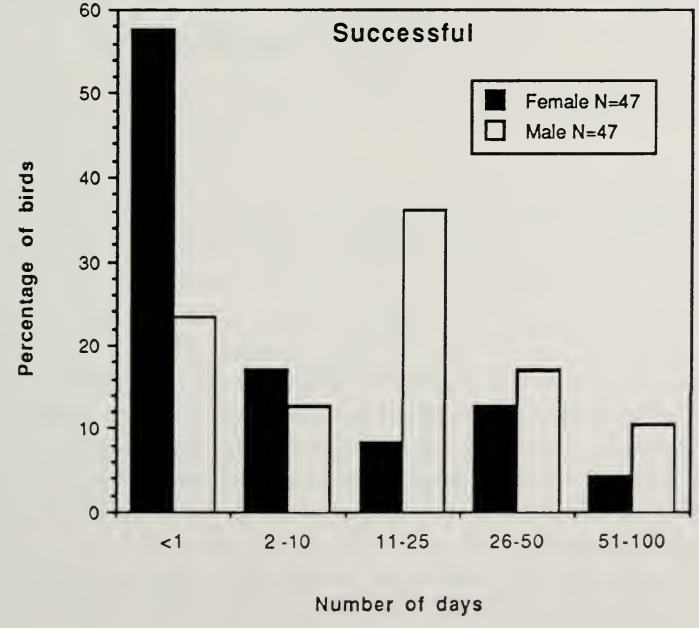
FIG. 4. Number of days that adult Snowy Plovers were detected at study sites after nests hatched (successful) or failed (unsuccessful).


Unsuccessful
Female N=41
Male N=28
Percentage of birds
50
40
30
20
10
0
<1
2-10
11-25
26-50
51-100
Number of days


Successful
Female N=47
Male N=47
Percentage of birds
60
50
40
30
20
10
0
<1
2-10
11-25
26-50
51-100
Number of days

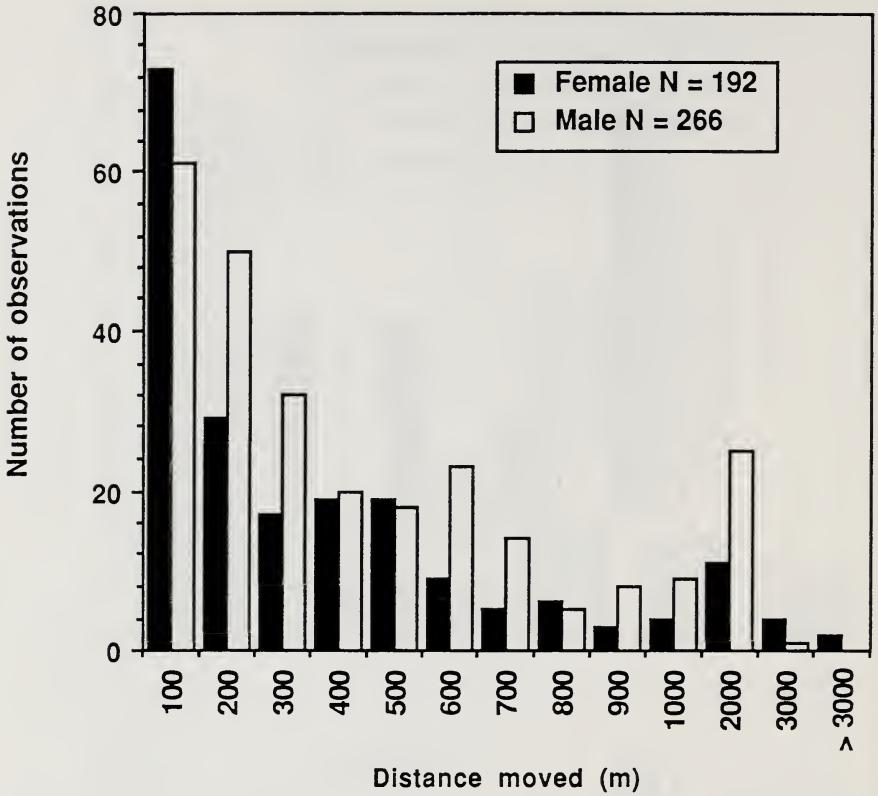


FIG. 5. Distances travelled by foraging or roosting Snowy Plovers away from active nests.

observations), while males were found as far as 2030 m (median = 272 m, 25%–75% quartiles = 110–580 m, N = 266). There was no intersexual variation in distances travelled (Mann-Whitney *U*-test = −1.2, N_1 = 60, N_2 = 53, P = 0.22) (Fig. 5).

The daytime incubation chronology differed between the sexes (G^2 = 23.2, 6 df, P = 0.001; Fig. 6). Females tended to incubate during the morning hours, while males often incubated in the mid-afternoon and late evening. Males and females often would exchange incubation duties on hot afternoons at short intervals (i.e., 10–15 min). In addition, males often would relieve females at dusk, when females were observed foraging together in small flocks. No attempts were made to quantify nocturnal incubation behavior.

Clutch size.—Modal clutch size was three eggs (93.3% of 327 clutches). There were 18 nests with a clutch size of two eggs, three nests

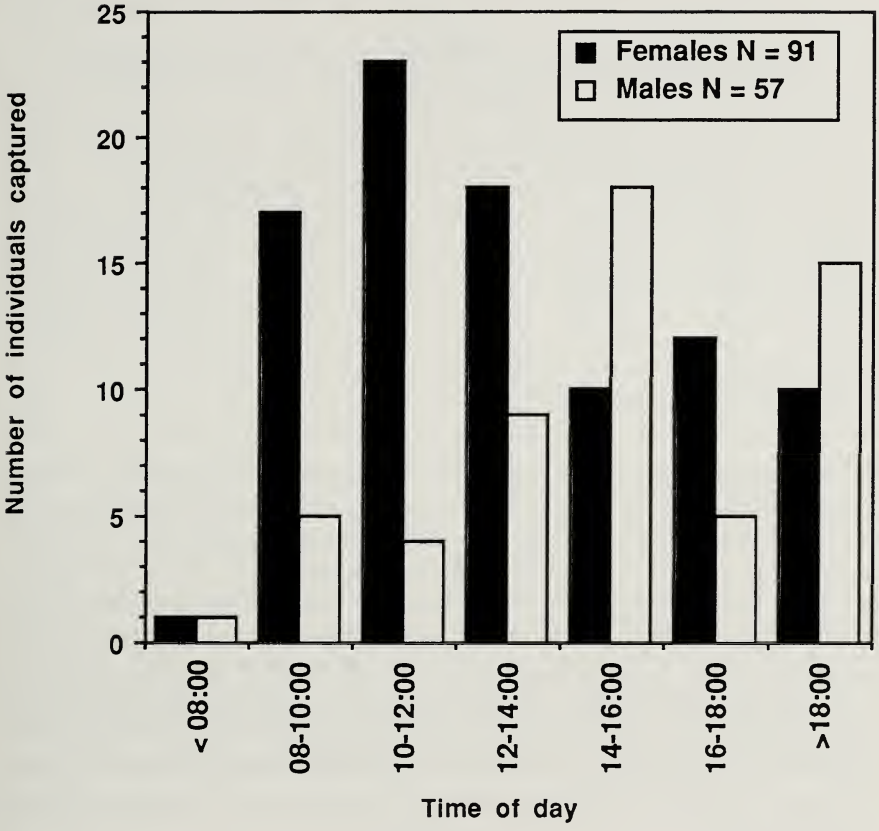


FIG. 6. Intersexual variation in daily incubation chronology of Snowy Plovers based on capture times of incubating adults.

with four eggs, and one nest with five eggs. There was no annual variation in clutch size over the four years of the study (G^2 = 7.5, 9 df, P = 0.58), and clutch size was similar between the two study sites (G^2 = 2.3, 3 df, P = 0.52).

Pair retention, double-brooding and polyandry.—Snowy Plovers in Utah did not exhibit mate fidelity between years. I documented only one occasion when the same pair remated between years, based on 123 nest attempts for 30 pairs initially banded. The pair that remated was originally banded at Layton on an unsuccessful nest in 1990. In 1991, the female mated with another male at Howard Slough, while the original male was seen only once at Layton marsh. In 1992, the 1990 pair successfully nested together at Howard Slough.

I twice documented double-brooding within the same year. One banded

TABLE 1
ANNUAL VARIATION IN SNOWY PLOVER NEST SUCCESS AT TWO STUDY SITES AT GREAT SALT LAKE

	Howard Slough				Layton Marsh			
	Mayfield method[a]				Mayfield method			
Year	Mean	95% CI	Apparent success	N	Mean	95% CI	Apparent success	N
1990	0.492	0.27–0.84	0.611	18	0.381	0.28–0.59	0.623	53
1991	0.197	0.10–0.38	0.314	35	0.113	0.06–0.20	0.247	73
1992	0.445	0.33–0.59	0.594	79	0.129	0.07–0.24	0.236	55
1993	0.054	0.11–0.17	0.133	30	0.345	0.17–0.70	0.471	71

[a] Based on Mayfield (1961) and Johnson (1979).

male at Layton marsh (mated with an unbanded female) had a clutch hatch successfully on 5 May 1991 and was last seen with this brood on 24 May. This male was then observed building a scrape on 7 June and incubating a second clutch, with an unbanded female, from 13 June to 10 July. Since neither female was banded, I do not know if the female represented one or two individuals. In the other instance, the one-day-old brood of a banded pair died after a cold rainstorm at Howard Slough on 8 May 1993. The female remated with a new banded male, although her original mate was still alive, and initiated a second nest on 10 June. This second clutch was lost to a predator on 20 June. This latter case was also the only example of within-year sequential polyandry I documented during this study.

Nest success.—Estimates for mean annual nest success (Mayfield method) ranged from 5.4 to 49.2% at Howard Slough and 11.3 to 38.1% at Layton marsh (Table 1). Nest success varied widely from year to year, and the annual fluctuations were not consistent between the two study areas ($G^2 = 43.5$, 3 df, $P < 0.001$; Table 1). Mammalian predators were responsible for most nest failures (42%, N = 188) based on tracks and scat near nests. Avian predators were documented taking 6.9% of all nests, flooding totalled 13.8% of nest losses, and unknown predators (37.3%) accounted for the remainder of the losses. I often could not determine the type of predator because both mammalian and avian predators will remove eggs from nests (Rearden 1951; G. Page, pers. comm.), and the soil was usually too hard for track retention. However, red foxes were probably the primary predators during this study, accounting for 90% of all documented mammalian nest depredations, and because red foxes were the most common predator at both study sites all four years. Striped skunks were observed only in 1993, and raccoons were also rare until

TABLE 2
ANNUAL VARIATION IN AVERAGE SNOWY PLOVER BROOD SIZE BY AGE CLASS

	1990		1991		1992		1993			
Age[a]	$\bar{x} \pm$ SE	N	$\bar{x} \pm$ SE	N	$\bar{x} \pm$ SE	N	$\bar{x} \pm$ SE	N	F^b	P
1	2.3 ± 0.1	50	2.3 ± 0.1	49	2.3 ± 0.1	53	2.1 ± 0.2	23	0.2	0.89
2	2.3 ± 0.1	22	2.2 ± 0.2	36	2.1 ± 0.1	71	2.0 ± 0.2	36	0.9	0.42
3	2.2 ± 0.2	18	1.9 ± 0.2	27	2.1 ± 0.1	50	2.0 ± 0.2	31	0.5	0.66
4	2.0 ± 0.1	57	1.9 ± 0.1	36	1.8 ± 0.1	54	1.8 ± 0.1	57	0.7	0.56

[a] Brood age in weeks.
[b] ANOVA, comparing brood size among years by brood age.

1993. California Gulls (*Larus californicus*) appeared to prey on plover nests only where gulls roosted, and I never observed gulls actively searching for plover nests. Common Ravens (*Corvus corax*) depredated ten nests, all at Layton marsh, where flocks of up to 65 ravens were occasionally observed foraging in plover nesting habitat. In contrast, ravens were rarely observed foraging at Howard Slough.

Fledging success.—There was no apparent annual variation in the number of chicks in the four age classes (Table 2), and fledging rates did not appear to vary annually with an average of 1.87 chicks per brood for successful nests (Table 2). I had a relatively difficult time following individual broods for long periods of time. Therefore, I was unable to estimate the percentage of broods that did not successfully fledge any young.

DISCUSSION

The duration of the breeding season for Snowy Plovers nesting in Utah (14 weeks) was closer in length to that reported from coastal California (Warriner et al. 1986) than from Kansas (Boyd 1972, Grover and Knopf 1982). Plovers breeding in Utah are all migratory (Page et al. 1995). In contrast, Snowy Plover populations in coastal California consist of both migratory and year-round resident birds and have egg-laying periods encompassing 16 weeks from 23 March to 13 July (Warriner et al. 1986). Birds nesting in the Great Plains are also migratory, and most nests are initiated during a six-week period from 15 May to 30 June; there is one early record from 22 April (Boyd 1972, Grover and Knopf 1982). Given the relatively short breeding season in the Great Plains, it is not surprising that birds breeding there appear to be exclusively single-brooded and monogamous (Boyd 1972).

The mating system of Snowy Plovers breeding in northern Utah appears to resemble that of coastal California populations (Warriner et al.

1986; Stenzel et al. 1994) more than those in the Great Plains (Boyd 1972, Grover and Knopf 1982). Four lines of evidence suggest that Snowy Plovers nesting in Utah are regularly double-brooded and sequentially polygamous, although I found little direct evidence to support the existence of either strategy at Great Salt Lake. First, I documented two examples of double-brooding. Second, plovers in Utah exhibited uniparental care of broods, with only males taking care of broods one week after hatching. Third, based on a 31-day laying and incubation period (Page et al. 1985, Warriner et al. 1986) and the fact that only males care for broods, there was ample time for females to produce two clutches during the 14-week nest initiation period in northern Utah. Finally, the nest initiation chronology suggests there are two or three distinctive peak initiation periods (Fig. 2). Based on studies conducted in California, the peak during the second week of June potentially represents successful females initiating second clutches, while the early July peak represents successful males initiating second clutches (G. Page, pers. comm.).

My inability to find the nests of the majority of the banded birds resighted at the study sites (i.e., 84.3% of 108 females, 81.0% of 116 males; Fig. 3) may have been due to at least five factors. First, an unknown percentage of both sexes could have been "floaters" (i.e., nonbreeding birds that did not nest that year; see Beletsky 1992). Second, many females and males (44.0% and 28.7%, respectively) were observed only on one occasion within a breeding season. This suggests that a substantial proportion of the plovers observed at the study sites were transients from other locations at Great Salt Lake or an even larger region, trying to find either suitable breeding habitat or potential mates. A similar strategy has been reported among Spotted Sandpipers (*Actitis macularia*), although their search for breeding sites appears to be more restricted to the postbreeding dispersal period (Reed and Oring 1992). Third, plovers in Utah often spent most of the day foraging over one km from their nests (Fig. 5), with the likely result that many nests went undiscovered. Fourth, breeding plovers were often extremely secretive around their nest (Boyd 1972, Warriner et al. 1986, Paton 1994). For example, three color-banded breeding adults (1 female and 2 males) were resighted only when they were captured on their nests but were not seen before or afterwards. Their secretive nature made it extremely difficult to determine which individual bird was associated with each nest. Finally, large numbers of plovers used each study site. This was exemplified by the fact that although I banded 256 adults at both sites, banded birds often accounted for less than ten percent of the birds observed on any given day (Paton 1994). Thus when nests were found, they were often those of unbanded birds.

In contrast to results from coastal California (Warriner et al. 1986),

Kansas (Boyd 1972) and the European subspecies in Germany (Rittinghaus 1956), I found little evidence that Snowy Plovers in northern Utah commonly renested in the immediate vicinity of their failed nest. Reasons for the apparent absence of renesting in Utah are unclear. It is possible that with so much plover nesting habitat available to breeding birds around Great Salt Lake from 1990 to 1993, pairs that attempted to renest moved off the study sites to maximize the probability of a successful nesting attempt. Snowy Plovers are known to be highly mobile, with females often moving over 50 km between nests (Stenzel et al. 1994). However, at most breeding sites in western North America, they are known to renest soon after clutch loss (G. Page, pers. comm.). This suggests that my inability to identify the owners of many nests was the primary reason I rarely documented renesting.

Apparent nest success rates found during this study (13.3%–62.3%) were lower than reported for plovers in Oklahoma (38–73%; Grover and Knopf 1982), Kansas (55%–60%; Boyd 1972), coastal California (50%; Warriner et al. 1986), and eastern, interior California (59.3%; Page et al. 1985). Of all these studies, Utah was the only area where red foxes were the dominant predator. A recent invasion of red foxes in coastal California has had a significant negative impact on plover nest success (G. Page, pers. comm.). Red foxes are the primary predator of Piping Plovers (*C. melodus*) nesting along parts of the Atlantic coast (Patterson et al. 1991) and have forced managers to adopt short-term solutions such as fencing off individual nests to reduce depredation problems (Rimmer and Deblinger 1990). However, long-term management strategies need to be developed to minimize nest depredation by red foxes on ground-nesting species throughout North America.

ACKNOWLEDGMENTS

I thank my field assistants Jack Dalton, Jennifer Levy, and Craig Kneedy. I thank Thomas Edwards, Jr., Frank Messina, Kimberly Sullivan, Mark Ritchie, John Kadlec, Tex Sordahl, and Gary Page for comments on earlier drafts of this manuscript. Val Bachman and Justin Dolling of the Utah Division of Wildlife Resources helped with access to refuge lands. Financial support for this study was provided by the Utah Division of Wildlife Resources, Native Wildlife Section.

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EASTERN BLUEBIRDS ARE ATTRACTED TO TWO-BOX SITES

JONATHAN H. PLISSNER[1] AND PATRICIA ADAIR GOWATY[2]

ABSTRACT.—In early March, just prior to the onset of the breeding season, responses by Eastern Bluebirds (*Sialia sialis*) to playbacks of the territorial song of conspecifics are more likely on sites with two nest boxes rather than one. One or two boxes were placed randomly at potential territorial sites during early winter; so responsiveness is not explained by territoriality of the previous season. Explanations for our observations include that bluebirds prefer potential territorial sites with two boxes because of increased habitat quality or that bluebirds locate two-box sites more readily than one-box sites. We infer from our result that potential territorial sites with two nesting boxes are more attractive to bluebirds than sites with only one nesting box. *Received 6 Sept. 1994, accepted 1 Dec. 1994.*

Nest site limitation is common for secondary cavity nesting species, which do not excavate their own cavities but use cavities produced by other species or those created by death and disease of trees. For Eastern Bluebirds (*Sialia sialis*) limited availability of cavities suitable for breeding accounts for the reduction of their populations in many areas (Zelany 1976), as suggested by the increases in their numbers in areas where nest boxes are provided. Besides affecting the overall numbers of nesting bluebirds, variation in nest site numbers and distributions is expected to have other effects on the behavior of bluebirds, including effects on the sociographic mating pattern and genetically effective mating system (Gowaty 1980). Here we describe an experiment designed to evaluate if variation in number of nesting boxes on a potential territorial site affects the "attractiveness" of potential territories to bluebirds.

We reasoned that if potential territories with more than one cavity suitable for nesting are more attractive to bluebirds than potential territories with one cavity, bluebirds should show evidence of earlier settling or stronger territoriality on two-box than on one-box sites. We therefore predicted that (1) responses to playbacks of territorial song will be greater on two-box than on one-box sites, (2) the difference in time between the onset of playback and response by bluebirds will be less on two-box than on one-box sites, and (3) onset of nesting activities will be earlier on sites with two nesting boxes than on those containing a single nesting box.

METHODS

In January 1985, we erected nest boxes on 43 sites on Clemson University properties in Pickens and Anderson counties in northwestern South Carolina. PAG chose sites for place-

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ment of nesting boxes within well-known study areas if those sites had been used as territories successfully by bluebirds anytime during the field seasons of 1977–1982. Thus we were confident that the sites at which we placed boxes were suitable for nesting by bluebirds. We assigned these sites randomly to two treatments such that each study area had approximately equal numbers of sites submitted to each treatment: at 20 of the sites we erected only a single nesting box. At 23 sites we erected two boxes within 24 m ($\bar{x}$ = 17.3 m ± 3.37 SD) of one another, distances that easily allow defense of both boxes on a site by a lone male or a pair of bluebirds.

During the first week of March before nesting activity had begun, we conducted playback trials at each site, using a recorded territorial song of an adult male bluebird. We set the tape player within 10 m of nesting boxes on one-box sites or midway between the boxes at two-box sites. We allowed tapes to play for a maximum of 10 min at each site. If bluebirds approached within 10 m of the boxes during the ten-minute period and behaved as though they were aware of the tape, i.e., if they approached the tape player, sang, or wing-flicked and chattered near a nesting box (Krieg 1971), we scored the trial as a response. If no bluebirds appeared by the end of the 10 min period, we scored the trial a "non-response." For bluebirds which responded to the tape, we also recorded their numbers and sexes and the latency of response from the time we started the tape. We censused all nesting boxes at least twice a week to determine occupancy and dates of onset for nest building, egg laying, hatching, and fledging.

All statistical tests are two-tailed. We derived power of tests from tables in Cohen (1988). We report power for small (Student's *t*, d = 0.2; *G*-test, w = 0.1) and large (Student's *t*, d = 0.8; *G*-test, w = 0.5) effect sizes as discussed by Cohen (1988).

RESULTS

Response to taped territorial calls was significantly associated with the number of boxes on a site (Fig. 1). At two-box sites, we recorded 13 responses, while at one-box sites there were only two responses (G = 11.123, df = 1, $P < 0.001$). The two responses at one-box sites were by males and females together. Three (23%) of the responses in two-box sites were by males alone; the others were by both males and females.

Overall (N = 15), the mean latency to response was 1.94 ± 2.36 min. However, there was no statistically significant difference in latency for birds that responded at one-box ($\bar{x}$ = 1.0 min) or two-box ($\bar{x}$ = 2.1 min) sites (Student's $t = -0.5937$, df = 13, $P = 0.5629$; but power for larger effect ≤0.3). When we assigned latencies (= 11 min) for non-response trials, the latency for one-box sites (N = 20) was $\bar{x}$ = 10 min ± 3.1 SD and $\bar{x}$ = 6 ± 4.9 SD for two-box sites (N = 23), a significant difference (Student's t = 3.1844, df = 41, P = 0.0025).

Twelve (52%) two-box and nine (45%) one-box sites had early-season nests begun in boxes during mid- and late March. However, there was no apparent statistical association between the number of nest boxes on a site and the likelihood of early season use by bluebirds (G = 0.216, df = 1, $P > 0.50$; $\text{power}_{w=0.1} = 0.10$, $\text{power}_{w=0.5} = 0.91$). Over the entire field season (March–September), there were 94 nesting attempts in boxes on the experimental sites. Thirty-nine (41%) were in boxes on one-box

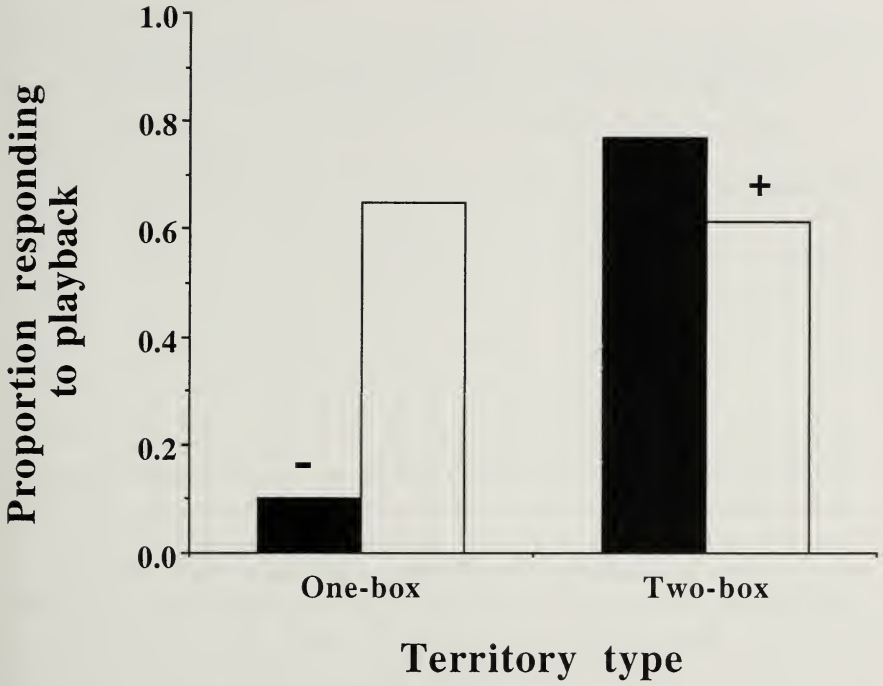

FIG. 1. Frequency histogram of observed (solid bars) and expected (open bars) proportions of playback trial responses by Eastern Bluebirds at potential territorial sites with one and two nesting boxes. The signs above the bars indicate the direction of the difference between observed and expected proportions.

and 55 (58%) were in boxes on two-box sites. The expected proportions were 47% and 53%, respectively, based on the numbers of each type of site, and the observed proportions were not statistically different from these ($G = 1.1494$, df = 1, $P > 0.50$; $\text{power}_{w=0.1} = 0.16$, $\text{power}_{w=0.5} > 0.99$).

Mean dates of onset of nest building and of the laying of first eggs were earlier for two-box territories, although these differences were not statistically significant (Table 1; $\text{power}_{d=0.2} = 0.09$, $\text{power}_{d=0.8} = 0.68$). We also found no statistical differences in the numbers of eggs laid and hatched or nestlings fledged (Table 1; $\text{power}_{d=0.2} = 0.16$, $\text{power}_{d=0.8} = 0.97$).

DISCUSSION

The single significant difference between one- and two-box sites that we observed was in responses to taped territorial calls played before the

TABLE 1
COMPARISONS OF PHENOLOGY AND DEMOGRAPHY FOR BLUEBIRDS NESTING IN ONE- OR TWO-BOX TERRITORIES

Variable	Treatment	N	$\bar{x}$	SD	t	df	$P > \|t\|$
Nest building begun[a]	One-box	18	12 March	36.4	0.505	37	0.617
	Two-box	21	6 March	38.9			
First eggs[a]	One-box	18	24 March	29.1	0.283	37	0.779
	Two-box	21	21 March	31.1			
Clutch size	One-box	39	4.2	1.69	1.589	92	0.116
	Two-box	55	3.6	1.86			
Brood size	One-box	39	3.2	1.78	1.205	92	0.231
	Two-box	55	2.7	2.08			
Number fledged	One-box	38	2.6	1.82	1.066	89	0.289
	Two-box	58	2.2	2.12			

[a] Includes dates for first nests only.

onset of breeding activities in early March. Because all of the sites had been used by bluebirds in previous seasons, the differences cannot be attributed to general habitat quality other than nest box number. Because most of the sites lacked nesting boxes, and were therefore uninhabited by bluebirds during the immediate two preceding seasons (1983–1984) and because sites were randomly assigned to one- or two-box treatments, the differences in responses cannot be attributed to previous-season territoriality. We assume that bluebirds were equally likely to have spent the fall and early winter on or nearby our experimental one- and two-box sites, because these boxes were erected randomly early in the winter period. However, our data may indicate stronger winter territoriality at two-box sites. We conclude that the likelihood of response by bluebirds to taped territorial calls is associated with the number of nesting boxes on a site.

Our data offer little or no support for our other two predictions. Latency to response did not differ on the two sites, an observation that may be due to the small numbers of birds responding on the one-box sites. On the other hand our experimental protocol defining the end of the trial after the tape had played for ten minutes may have been too short to discern most latencies associated with one-box sites. In fact, at one one-box site bluebirds did respond, but only after the tape had played for eleven minutes. At best, our prediction that latencies to response would be less in two-box sites is equivocably supported. Dates for first nest building activity and first eggs did not differ on one- and two-box sites, so our third prediction is clearly not supported. The onset of nest building and egg

laying probably depends on other environmental factors other than the number of nest boxes on a defended site, so failure to support our third prediction does not modify our observation that response to taped territorial calls was associated with the number of nesting boxes on sites representing potential territories.

Three possible explanations for this result occurred to us: (1) Bluebirds preferentially selected two-box over one-box sites as potential territories, so their responsiveness may have been evidence of winter territoriality or incipient breeding season territoriality associated with the quality of the sites. (2) Bluebirds found two-box sites more readily than one-box sites. (3) Two-box sites exerted a super-stimulus, such that stronger territorial defense was elicited at two-box sites than at one-box sites.

If bluebirds prefer two-box sites as potential territories, the preference may indicate that two-box sites, all else being equal, are potentially higher quality territories. Although higher territory quality could translate to higher reproductive success per breeding attempt, our data indicate that immediate reproductive success did not vary at one- and two-box sites. Quality of territory could be associated with additional mating opportunities for males, a prediction not supported by observations at these territories (Gowaty and Emlen, unpubl. data). Territory quality could be associated with additional nesting opportunities for males and females that might otherwise have to undertake a longer distance breeding dispersal if the suitability or quality of an original nesting site degraded or declined, a prediction also not supported by our current data (Gowaty and Plissner, in press). In any event, the hypothesis that two-box sites may represent higher quality potential territories than one-box sites predicts that two-box sites will be more vigorously contested than one-box sites.

Bluebirds may find two-box sites more readily than sites with only one box. At all seasons of the year (Allen 1988) and at all ages (pers. obs.) bluebirds examine cavities, a behavioral trait associated with nest-site limitation. If bluebirds imprint on the characteristics of nest sites and use old nest site characteristics in their searches for new nest sites, a two-box site might be more readily found in comparison to one-box sites in that potential cues might be doubled. This could be especially so for bluebirds whose natal site or previous breeding site was a nest box. Certainly if their searches for cavities are random searches and if an important cue to territory suitability is the presence of a cavity, sites with two nesting boxes will be found more readily than sites with one. This hypothesis predicts that territories on sites with two nesting boxes may suffer more intrusions by non-territorial birds than territories on sites with one nesting box.

The hypothesis that two-box sites elicit greater responsiveness because

the usual stimulus is doubled seems unlikely, because neither latency times nor response intensity seem to vary in one- and two-box sites; i.e., if birds responded at all, they seemed to behave similarly in one- and two-box sites. Responsiveness and response intensity, however, may be uncoupled such that the intensity of response is associated only with the characteristics of the intruder and not of the resource being defended. We nevertheless expect that latency should be coupled with responsiveness if the superstimulus hypothesis was true.

We conclude, then, that bluebirds respond to taped territorial song more when the song is played on potential territorial sites with two nesting boxes than they do on sites with only one box. We infer from this that two-box sites are more attractive potential territories than one-box sites. We are unable to attribute this attractiveness to preferences for higher quality territories or to the increased stimulus value of territories with two rather than one box. Indeed, our explanations for our observations are not mutually exclusive.

These hypotheses to explain our observations predict that territories on two-box sites will suffer higher intrusion rates by conspecifics than territories on one-box sites. Harris (1977) reported higher rates of territorial aggression by breeding resident Tree Swallows (*Tachycineta bicolor*) when nesting boxes were 1 m apart than when they were separated by 30 m. Also, Meek and Robertson (1994) observed more intrusions of Eastern Bluebird territories by Tree Swallows at territories containing two nesting boxes than at those with single boxes. In a study of nest guarding, Gowaty et al. (1989) found that both males and females remained closer to boxes during nest-building and egg-laying periods, when territories are most susceptible to usurpation and conspecific nest parasitism, but not during incubation or while nestlings were present.

Extrapolation from our observations also suggests that bluebirds may initially appear in greater numbers in areas with many rather than fewer nesting boxes. A test of this idea would vary the density of nesting boxes randomly over areas that currently have few or no bluebirds. The hypothesis would be supported if significant differences in the numbers of bluebirds initially nesting were found in areas with higher densities of nesting boxes. Finally, if bluebirds are more attracted to two-box sites than one-box sites, managers interested in attracting bluebirds might have greater success associated with potential territories containing two nesting boxes.

ACKNOWLEDGMENTS

We thank Tracey Williams for her help in conducting these trials, Steve Emlen and Natalie DeMong Emlen for their help in erecting nest boxes, and Dave Tonkyn, Mimi Wolok, and

Dick Conner for comments on the manuscript. This research was supported by grants from the National Geographic Society (3006-84) and The National Science Foundation (BSR-8417500), both to PAG.

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Wilson Bull., 107(2), 1995, pp. 296–305

PLASMA CORTICOSTERONE LEVELS IN TWO SPECIES OF *ZONOTRICHIA* SPARROWS UNDER CAPTIVE AND FREE-LIVING CONDITIONS

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ABSTRACT.—We compared the daily plasma corticosterone (B) profiles in captive and free-living White-throated Sparrows (*Zonotrichia albicollis*) and White-crowned Sparrows (*Z. leucophrys*) during their non-breeding period. Neither sparrow species exhibited significant diel rhythms in the levels of corticosterone in captivity or under natural conditions, although the variations were suggestive of a rhythm. In each species, secretory profiles differed significantly between captive and free-living birds with mean B levels being 2–3 times higher in captive birds than in free-living individuals, despite the fact that captives had been "acclimated" for 35 days prior to sampling. Furthermore, mean B levels were two to four times higher in White-throated Sparrows under captive and free-living conditions than in White-crowned Sparrows under the same conditions. Our results indicate the need to use caution when (1) extrapolating such data obtained from captive individuals to those under natural conditions and (2) extrapolating data regarding B from one species to another. *Received 28 July 1994, accepted 1 Dec. 1994.*

Environmental stimuli may affect the concentrations and secretory patterns of hormones, such as the "stress-related" corticosteroid hormones, which can dictate physiological changes in organisms. In birds, the principal corticosteroid hormone is corticosterone (hereafter "B") (Assenmacher 1973). Perception of stressful stimuli markedly enhances the rate of B secretion through the actions of adrenal cortical stimulating hormone (ACTH), resulting in increased levels of B in the blood (Siegel 1971, 1980). In birds, this cause-effect relationship has been shown to occur in response to a variety of stressors (for review see Harvey et al. 1984), including thirst and starvation (Freeman et al. 1980, Scott et al. 1982), pollution (Holmes and Gorsline 1980), weather and temperature (Brown and Nestor 1973, Wingfield 1988), capture, handling and immobilization (Edens and Siegel 1975; Wingfield et al. 1982; Wingfield et al. 1992) and social stress (Gross and Siegel 1973, Satterlee et al. 1982).

Much of the current data on avian B profiles has been obtained from studies involving domesticated species or from wild species maintained in captivity (see references above). Data obtained from such studies are presumed to be similar to those which would be obtained from birds in

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nature. Since confinement itself or exposure to humans may be a stressor which might elevate B concentrations (Suarez and Gallup 1982, Hemsworth and Barnett 1989), especially in wild birds, the validity of these extrapolations needs to be tested. Determination of basal B levels is important in order to evaluate properly stress induced increases of B as well as for interspecific comparisons. Our first objective was to determine the basal B profiles of two species of sparrows (genus *Zonotrichia*) under natural conditions and compare these levels to birds acclimatized to captivity.

Seasonal variations in the recurring daily secretory profile of B have been observed in at least two avian species, the White-throated Sparrow (*Z. albicollis*) (Dusseau and Meier 1971) and the Garden Warbler (*Sylvia borin*) (Schwabl et al. 1991). Based on Dusseau and Meier's (1971) findings, Meier and Fivizzani (1975) proposed that the daily variations in B concentration occurring in different seasons reflects the dynamics of neuroendocrine mechanisms which directly control various aspects of seasonality in migratory birds, including premigratory fattening, migratory readiness, and breeding condition. Meier's hypothesis is supported primarily by studies of White-throated Sparrows maintained under captive conditions. In a similar study of the closely related White-crowned Sparrow (*Z. leucophrys*), Vleck et al. (1980) did not detect a recurring daily variation of B concentration. Thus, the second objective of our study was to compare the daily secretory profiles of B of these two congeners.

METHODS

White-throated Sparrows were mist-netted near Baton Rouge, Louisiana, on 24 and 25 January 1987 and placed in an outdoor aviary at Louisiana State University, Baton Rouge. White-crowned Sparrows were mist-netted near Charlotte, Texas, between 31 January and 2 February 1987, transported to Baton Rouge on 2 February, and placed in separate sections of the aviary housing the White-throated Sparrows. Both species were residing on their wintering grounds when captured. The outdoor aviaries in which the captive sparrows were maintained measured 6 × 4 × 4 m and were exposed to the natural local climate and photoperiod. At no time were birds exposed to any direct artificial lighting. Each enclosure held approximately 15 birds and contained numerous perches and abundant cover. A total of approximately 60 birds of each species were held in captivity for these experiments. During the acclimation period the aviary was entered only briefly once every three days to replenish food and water supplies. Water and a commercial bird seed (millet, sunflower seeds, corn mash) were provided ad libitum on the floor of the cage.

All birds were maintained under these conditions for approximately 35 days prior to having blood drawn for B assay (30–35 days is often used as an acclimation period prior to sampling captive wild birds). Blood samples were collected from captive White-throated Sparrows between 4 and 6 March and captive White-crowned Sparrows between 10 and 16 March. On each day, blood samples were collected from birds during six 1-h time periods (02:00–03:00, 06:00–07:00, 10:00–11:00, 14:00–15:00, 18:00–19:00, and 22:00–23:00). Individual birds were selected for blood collection by allowing a few individuals from a larger

group of birds to disperse passively to unoccupied sections of the aviary where they were netted. Generally, only two birds were sampled during each of the one-hour time periods per day, and sampling was done in more than one of the periods per day. This procedure permitted us to cause only minimal disturbance to the main group of birds and to the target bird prior to sampling blood. No bird was sampled more than once, and only those blood samples which were obtained within 60 sec of our initial effort to net a bird were assayed for B. Using only samples withdrawn during the initial 60 sec ensures that blood B levels do not reflect the stress of capture and handling associated with the blood sampling procedure (Wingfield et al. 1982, Schwabl et al. 1991). Blood was drawn by heart puncture, placed in heparinized tubes and kept on ice until plasma isolation.

For both species, blood samples were obtained from free-living birds at the same location where captive birds had been previously captured. Samples were collected during four one-hour time periods, beginning at first light and ending at dark (06:00–07:00, 10:00–11:00, 14:00–15:00, 18:00–19:00). Free-living White-throated Sparrows were collected between 25 February and 4 March and free-living White-crowned Sparrows between 7 and 9 March 1987. Individuals were collected from wintering flocks using .410 or .22 gauge bird shot. All possible efforts were taken to minimize disturbing birds while approaching flocks prior to collection and only one bird was collected in a particular flock per day to insure no residual stress from our prior disturbance. Blood samples were obtained by heart puncture within 60 sec of downing a bird, placed in heparinized tubes, and kept on ice until isolating and freezing plasma (within 2 h of collection). Birds were sexed by inspection of gonads and were deposited as specimens in the Louisiana State Univ. Museum of Natural Science.

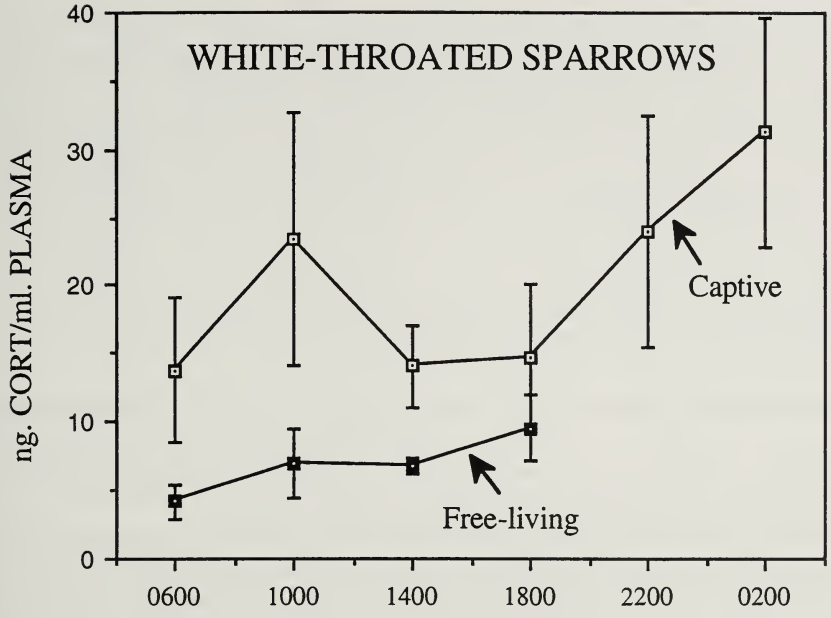
Plasma was isolated from whole blood by centrifugation (10,000 × g for 60 sec), decanted and frozen at −20°C until assayed for B. The B concentration of each sample was determined by a single batch radioimmunoassay (Satterlee et al. 1980). For assay protocol, sensitivity, extraction efficiency, and specific-binding properties see Satterlee et al. (1980). Statistical comparisons were made by ANOVA or Student's *t*-test.

RESULTS

The concentration of B ranged from 4.2 ± 1.3 ng/ml (mean ± SE) (06:00 h, N = 6) to 9.5 ± 2.4 ng/ml (18:00 h, N = 7) in free-living White-throated Sparrows and from 13.8 ± 5.3 ng/ml (06:00 h, N = 6) to 31.3 ± 8.4 ng/ml (02:00 h, N = 6) in captive White-throated Sparrows (Fig. 1). In White-crowned Sparrows the plasma B concentrations ranged from 0.6 ± 0.2 ng/ml (14:00 h, N = 6) to 1.6 ± 1.0 ng/ml (06:00 h, N = 7) in free-living birds and 3.1 ± 1.1 ng/ml (18:00 h, N = 6) to 6.3 ± 2.5 ng/ml (06:00 h, N = 6) in captives (Fig. 1b). Despite variations, there were no significant differences in B levels among time periods for either captive ($F_{5,30} = 1.039$, $P < 0.50$) or free ($F_{3,22} = 1.1044$, $P > 0.50$)

→

FIG. 1. Corticosterone (B) concentration (means and SE) by time of day for free-living and captive White-throated Sparrows and White-crowned Sparrows. Each point represents a sample of six individuals (except 10:00 and 18:00 in captive White-throated Sparrows, N = 7; and 06:00 and 10:00 in captive White-crowned Sparrows, N = 7). Note different scales on the y-axis.


WHITE-THROATED SPARROWS
ng. CORT/ml. PLASMA
40
30
20
10
0
Captive
Free-living
0600
1000
1400
1800
2200
0200

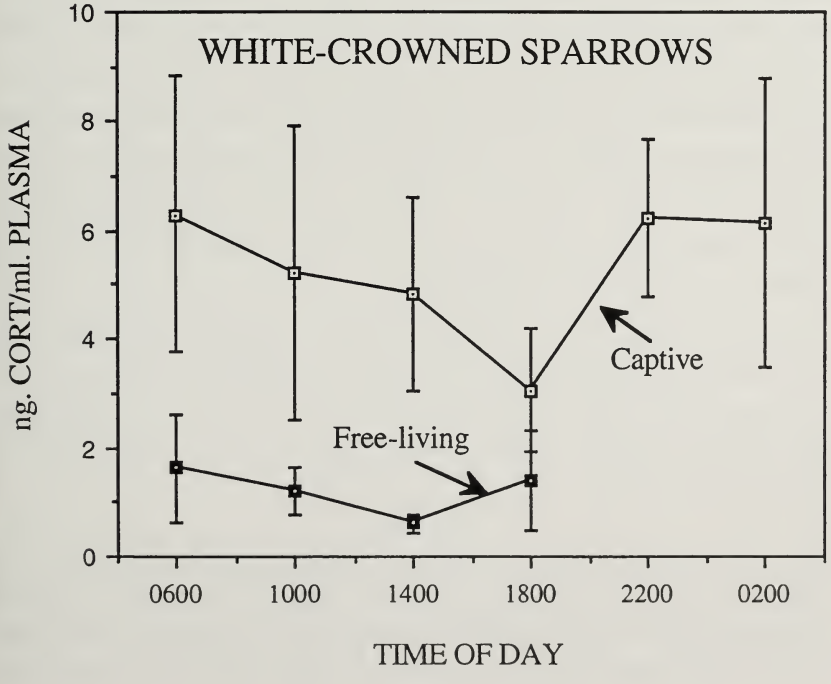

WHITE-CROWNED SPARROWS
ng. CORT/ml. PLASMA
10
8
6
4
2
0
Captive
Free-living
0600
1000
1400
1800
2200
0200
TIME OF DAY

TABLE 1

DAILY MEAN CORTICOSTERONE (NG/ML) FOR CAPTIVE AND FREE-LIVING WHITE-THROATED AND WHITE-CROWNED SPARROWS (N = SAMPLE SIZE)

Species[a]	Free-living mean ± SE	Captive mean ± SE
White-throated Sparrow	6.68 ± 1.0 N = 26	16.45 ± 2.9 N = 24
White-crowned Sparrow	1.16 ± 0.3 N = 26	4.93 ± 1.0 N = 24

[a] Species differed significantly under both treatments both between and within species, $P < 0.001$, *t*-test.

White-throated Sparrows, or captive ($F_{5,29} = 0.336$, $P > 0.75$) or free ($F_{3,23} = 0.5275$, $P < 0.75$) White-crowned Sparrows when tested by ANOVA. Furthermore there were no significant differences between B concentrations of males and females of either species.

Mean plasma B concentrations differed significantly between captive and free-living birds of the same species at most sampling times (Fig. 1) (*t*-test; $P < 0.05$). Corresponding values differed between captive and free-living birds, on average, by 260% for White-throated Sparrows and by 460% for White-crowned Sparrows (Fig. 1). A single daily-mean plasma B concentration was calculated for each experimental group by taking the mean of all values obtained between 06:00 and 18:00. B values from the 22:00–23:00 and 02:00–03:00 sample periods were not included in the daily-mean B concentration for captive birds since these comparable values were not available for free-living birds. The daily-mean B concentration was 250% and 430% greater in captive White-throated and White-crowned Sparrows than in their respective free-living counterparts (Table 1) (White-throated Sparrows, T = 3.20, $P < 0.003$; White-crowned Sparrows, T = 3.75, $P < 0.0008$).

Interspecific differences in daily-mean B concentration between these closely related congeners were also significant (Table 1). The daily-mean B concentration in free-living White-throated Sparrows was 580% greater than in free-living White-crowned Sparrows (T = 3.64, $P < 0.0009$), and 330% greater in captive White-throated Sparrows than in captive White-crowned Sparrows (T = 5.37, $P < 0.00002$).

DISCUSSION

Recurring daily variations in plasma B concentration have been detected in four domesticated species: Turkey (*Meleagris gallopavo*; Davis and Siopes 1988), Japanese Quail (*Coturnix coturnix*; Boissin and Assenmacher 1970, Assenmacher and Boissin 1972), Rock Dove (*Columba*

livia; Joseph and Meier 1973), and Domestic Fowl (*Gallus domesticus*; Webb and Mashaly 1985, Lauber et al. 1987). Similar variation was detected in two wild species maintained in captivity, White-throated Sparrow (Dusseau and Meier 1971, Meier and Fivizzani 1975) and Garden Warbler (Schwabl et al. 1991), but was not present in another wild species, the White-crowned Sparrow (Vleck et al. 1980). The occurrence of daily variations in plasma B levels in some species poses a problem for investigators if the levels of B are not consistently assessed at the same phase of the daily secretory profile. Furthermore, the fact that a daily variation of B concentration occurs in some species and is absent in others raises questions regarding the physiological significance of such hormone cycles. The period of the annual cycle also needs to be considered. We examined B levels at only one stage of the annual cycle which could very well explain our lack of significance.

Total plasma B concentration, as measured in the present study, includes B which is protein-bound and the bioactive fraction which is not protein-bound. It is possible that the plasma concentration of bioactive B could vary somewhat independently of the total plasma B concentration. However, Meier et al. (1978) examined this possibility in captive White-throated Sparrows and found that both total and bound plasma B varied similarly during the day. A close correlation between changes in plasma B level and relative concentration of protein-bound B has been observed in other species as well (Siegel et al. 1976, Kovács and Péczely 1983).

Significant daily variations of plasma B concentrations were not detected in captive sparrows of either species in this study. This observation is in accord with the findings of Vleck et al. (1980) for captive White-crowned Sparrows. However, our data are suggestive of a daily variation in B for both species.

At present, the cause of the differences of B concentration between captive and free-living birds of both species is unknown. To minimize external factors that might contribute to differences in B levels, we examined B concentrations in each experimental group of birds at the same times of day, and at the same time of year. Furthermore, free-living and captive birds of each species were sampled from the same locations.

Despite these precautions, we found highly significant differences in plasma B concentrations between captive and free-living birds for both species. This overall difference between captive and free-living birds is most likely due to increased ACTH release, possible due to a decreased level of B-feedback on corticotropin releasing factor (CRF) or increased adrenal sensitivity to ACTH, perhaps due to captive stress. Sustained differences in adrenal sensitivity to ACTH have been demonstrated in populations of chickens (Edens and Siegel 1975, Siegel 1973).

The differences in daily-mean B concentration between captive and free-living birds of the same species were especially surprising, given the length of the acclimation period. Wingfield et al. (1982) demonstrated a decrease in B levels after an acclimation period of two to three weeks for White-crowned Sparrows kept in small cages with one, two, or three individuals per cage. Our data suggest that our captive birds never fully "acclimated." In addition to the artificial stress imposed, there may have been additional social stressors of being in a confined space with other individuals. It is also possible that there was a residual stress effect from prior disturbances in the aviary, although we tried to minimize these as much as possible. Also, despite efforts to cause minimal disturbance, we may have induced some stress response during the sampling periods. One other possible explanation for the high B concentrations in "acclimated" birds may be change in diet. However, we don't believe that this was the case since seeds are the primary food for these sparrows in winter. There is no evidence to suggest that B concentrations are altered after subtle changes in diet. Furthermore, we did not observe any overt behavioral or physiological adversity in either species during the study period.

Although B concentrations were significantly different between captive and free-living birds, it is difficult to assess the biological significance of these differences in magnitude. Studies investigating the response of B to natural stressors in the wild and the potential impact that these resulting elevated B levels have on general fitness are long overdue.

The significant difference in B levels between these two congeners was unexpected. Both species are comparable in size, occupy similar habitats, and seem to exhibit similar behaviors while on the wintering grounds (P. P. Marra, pers. obs.). Furthermore, all birds were sampled at the same time of year at similar latitudes, and sample populations in both cases consisted of nearly equal numbers of male and female birds. Also, although we detected a species difference in the magnitude of increase in B levels owing to captivity, it seems unlikely that the difference found between free-living White-throated and White-crowned sparrows is "stress-related," unless these two species are continually subject to different degrees of stress in the wild. It is possible that the interspecific differences in B concentration reflect differences between the metabolic states of these species, perhaps caused by differences in habitat use, food availability, or reproductive readiness.

Given the dissimilarities among the daily profiles of B in the four experimental groups of birds examined, it seems unlikely that a particular secretory profile of plasma B serves a central role in determining the seasonal condition of these birds, at least at this phase of the annual cycle. This does not mean that a diel rhythm of B and other neurotransmitters

is not involved in establishing seasonality in birds. It is possible that a diel rhythm of plasma B is prominent at other phases of the annual cycle. Seasonal variations in plasma B levels have indeed been observed in several species (Meier and Fivizzani 1975, Wingfield et al. 1982, Hissa et al. 1983, Meier and Russo 1984, Wingfield 1985, Rehder et al. 1986).

To our knowledge, this is the first study in which daily profiles of plasma B have been compared between congeners, directly between birds in the wild and those maintained in captivity. Our results indicate significant differences not only between captive and free-living individuals within a species but also between congeners. Therefore, we suggest that extrapolations concerning B data be made with extreme caution. Furthermore, despite the lack of a significant daily variation of concentration, plasma B concentrations should be assessed, either at the same time or during predetermined times of day.

ACKNOWLEDGMENTS

The Frank M. Chapman Fund of the American Museum of Natural History funded this research. We thank Charles Schweppe for use of his property in Texas to conduct this study. A. H. Meier, J. V. Remsen, and D. Satterlee provided advice and use of their labs. Thanks to S. Cardiff and D. Dittman for help in collecting blood samples in Texas. This manuscript was improved by comments from S. Baird, R. Holberton, R. T. Holmes, J. I. Lovette, R. C. McClung, A. M. Perrault, C. M. Vleck, J. C. Wingfield, and one anonymous reviewer.

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Wilson Bull., 107(2), 1995, pp. 306–316

SOME FACTORS AFFECTING PRECISION OF THE TOTAL BODY ELECTRICAL CONDUCTIVITY TECHNIQUE FOR MEASURING BODY COMPOSITION IN LIVE BIRDS

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ABSTRACT.—Measurement of total body electrical conductivity (TOBEC) is a simple nondestructive method for estimating total body fat in live birds. Some published validations of the TOBEC technique have been promising, but other results, especially from species less than 100 g live mass, have indicated that TOBEC measurements add little to the accuracy of body fat estimates obtained with other nondestructive methods. We examined the accuracy of TOBEC body fat estimates for small birds by validating the technique on two passerine species, House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*). Lean mass explained only 57% of the variation in TOBEC for sparrows (average mass: 28.4 g) and 74% of the variation for starlings (average mass: 83.7 g). TOBEC measurements were not sufficiently precise to detect even large (i.e., 100%) changes in fat reserves of either sparrows or starlings. These results, when compared with validations for larger species, indicate that the precision of body composition estimates from TOBEC is very sensitive to subject size in relation to chamber size (coil diameter) of the TOBEC instrument; precision is greatest for subjects that nearly fill the chamber. We confirm that accuracy of TOBEC estimates of body composition in a variety of bird species depends on developing species-specific calibration curves; precision of estimates depends on use of a TOBEC chamber size appropriate to the study species. *Received 13 May 1993, accepted 10 Jan. 1995.*

The total body electrical conductivity (TOBEC) method is a noninvasive technique for estimating body composition in live animals (Walsberg 1988). Recently, the TOBEC technique has gained popularity among field ornithologists as a method for measuring fat reserves of free-ranging birds, either as a means of monitoring temporal changes in fat reserves of individuals or of assessing the relationship of fat reserves to subsequent survival and reproduction (Castro et al. 1990, Morton et al. 1991, Scott et al. 1991, Roby 1991, Skagen et al. 1993). Fat reserves can serve as a measure of physiological condition and can provide a useful index to habitat quality, efficacy of habitat management programs, and impacts of environmental contaminants (Blem 1990).

Research on energetic constraints for birds has been limited by the lack of a simple field technique for nondestructive measurement of fat re-

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serves. TOBEC analysis is attractive because the instrument can be used in the field, is simple to operate, and because measurements can be taken rapidly without invasive procedures. Although TOBEC analysis does not measure fat directly, total body fat can be estimated by subtracting TOBEC-estimated lean body mass from total body mass, determined by weighing the subject (see Harrison 1987, Malina 1987, Fiorotto et al. 1987, Boileau 1988, and Walsberg 1988 for details of operating principles). Alternatively, TOBEC has been used as an independent variable in multiple regression models to enhance the accuracy of body fat predictions from body mass and morphometrics (Morton et al. 1991, Skagen et al. 1993).

Although the SA-1 and SA-2 TOBEC analyzers (Em-Scan, Inc., Springfield, Illinois) are thought to be useful for estimating body composition of subjects as small as 10 g live mass (Walsberg 1988, Castro et al. 1990, Scott et al. 1991), body fat estimates for species at the lower end of this range (10–125 g) could be imprecise. With smaller subjects, there is less interaction between body water volume and the electromagnetic field (Em-Scan, Inc. 1989). Also, small subjects produce small TOBEC values, suggesting lower measurement precision.

The objective of this study was to evaluate the usefulness of the SA-1 TOBEC analyzer for measuring body composition in a wide range of passerines and other small birds. We sought to determine the precision of estimates of body fat and lean body mass for two passerines, European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*) and some of the factors that influence the precision and accuracy of these estimates. We wanted to identify a range of subject body sizes where estimates of body fat from the SA-1 TOBEC analyzer were sufficiently accurate to provide a useful index to body condition.

METHODS AND MATERIALS

We mist-netted both House Sparrows and European Starlings in the wild near Carbondale, Illinois and measured TOBEC using the SA-1 Small Animal Body Composition Analyzer (Em-Scan, Inc., Springfield, Illinois, USA). We measured TOBEC for 35 adult House Sparrows; 12 were measured during 4 February–4 March 1990 and 23 during 11–27 April 1991. We measured TOBEC for 63 European Starlings caught between 20 July and 9 August 1990 as they went to roost in the evening. Juvenile starlings were distinguished from adults by plumage color (Kessel 1951). We sexed live House Sparrows using plumage and live adult starlings using iris color and hackle feather morphology (Kessel 1951). Subjects were selected for TOBEC analysis so as to provide a wide range of body masses and approximately equal numbers of the two sexes.

We brought subjects indoors immediately after capture and weighed them to the nearest 0.01 g prior to TOBEC measurement. Subjects were inserted head first into a nonconductive nylon mesh stocking to restrict movement and hold the head and legs close to the body. The beak was inserted through a small hole in the end of the stocking to allow easy res-

piration. Consistent subject placement and restriction of movement are critical for repeatability of TOBEC measurements (Em-Scan, Inc. 1989). We positioned the subject near the center of the vertical axis of the measurement chamber using non-conductive acrylic spacing strips (Walsberg 1988, Em-Scan, Inc. 1989). A rubber band around the center of the body and the acrylic spacing strip provided additional restraint.

We used the protocol described by Roby (1991) to measure TOBEC of live subjects. The SA-1 (unlike the SA-2) continuously displays the impedance of the coil in real-time so that the subject can be centered in the electromagnetic field by moving it slightly in or out and recording the smallest value displayed. Immediately following TOBEC measurements, we humanely sacrificed subjects by cervical dislocation (AOU 1988), placed them in double plastic bags, and froze carcasses at −20°C. Prior to proximate analysis, carcasses were partially thawed, weighed, plucked, and reweighed to determine feather mass. The sexes of European Starlings were verified by inspection of gonads. Carcass analysis procedures followed those described by Roby (1991), except petroleum ether was used as the solvent system (Dobush et al. 1985).

We used a Lilliefor's test to test for normality of the data. We validated the TOBEC technique for each species by regressing TOBEC value against lean body mass determined by proximate analysis. Residuals about the regression line were used to investigate effects of other variables on TOBEC values (e.g., sex, total body fat, feather mass, total body water, % body water of lean mass). Least squares linear regression was used to predict lean mass from TOBEC value. We predicted body fat from TOBEC using the regression equation to estimate lean body mass and subtracting predicted lean body mass from live body mass. We used the inverse regression procedure (Sokal and Rohlf 1981:496) to establish 95% confidence limits for estimates of lean mass and body fat obtained by TOBEC analysis alone. Finally, we used multiple regression analysis with body fat as the dependent variable in order to evaluate the contribution of TOBEC, body mass, and sex for predicting total body fat (Morton et al. 1991, Skagen et al. 1993). Statistical analyses were conducted using SYSTAT 4.0 (Systat, Inc., Evanston, Illinois).

RESULTS

Average body mass, lean body mass, total body fat, and % body fat in the sample of House Sparrows used for the validation were normally distributed ($P > 0.05$, N = 35). Average total body mass for males (28.2 g, SD = 1.50, N = 22) and females (28.6 g, SD = 2.19, N = 13) was not different ($t = -0.65$, $P = 0.52$). Also, average body fat for males (0.99 g, SD = 0.33, N = 17) did not differ from females (1.26 g, SD = 0.51, N = 8; $t = 1.76$, df = 33, $P = 0.09$). The regression of % body fat as a function of total body mass was not significant ($r^2 < 0.02$, $F_{1,23} = 0.35$, $P > 0.05$, N = 25, $b = 0.094$).

Lean body mass explained 54% of the variation in TOBEC ($F_{1,33} = 38.3$, $P < 0.0005$, N = 35, $b = 1.37$). The coefficient of variation in TOBEC (a function of variation in the subject's position within the measurement chamber) for the six trials averaged 6.5% (SD = 2.80, range = 3.2–13.0%, N = 35). For 10 subjects, the standard deviation of % fat among aliquots was greater than 1.0%. When these 10 cases were eliminated, the significance of the regression ($r^2 = 0.55$, $F_{1,23} = 30.0$, $P <$

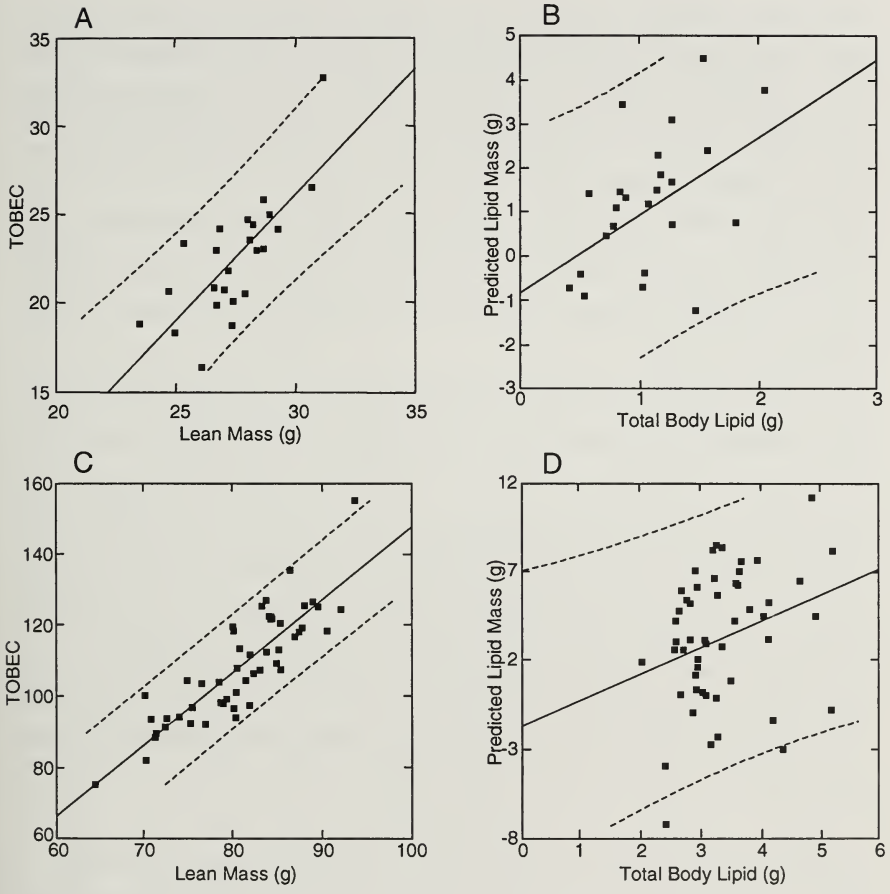

FIG. 1. (A) TOBEC as a function of lean body mass in House Sparrows. (B) TOBEC-estimated body fat as a function of extracted body fat in House Sparrows. (C) TOBEC as a function of lean body mass in European Starlings. (D) TOBEC-estimated body fat as a function of extracted body fat in European Starlings. Dotted lines represent 95% confidence intervals of the estimate of body fat from TOBEC in all graphs.

0.0005, N = 25, b = 1.43) was only slightly higher. For House Sparrows, TOBEC was related to lean body mass by: TOBEC value = −16.657 + 1.427(lean mass). The average residual of the regression of TOBEC on lean mass was 1.68 TOBEC units (SD = 1.33, range = 0.14–4.90, N = 25). The 95% confidence limits for TOBEC-estimated lean mass (derived by inverse regression) were 18.2–26.3 g for 23 g estimated lean mass, 23.4–30.5 g for 27 g estimated lean mass, and 19.0–44.2 g for 31 g estimated lean mass (Fig. 1A).

TOBEC-estimated body fat and solvent-extracted body fat were linearly-related, but the latter explained only 19% of the variance ($r^2 = 0.19$, $F_{1,23} = 5.26$, $P = 0.03$, N = 25, $b = 1.75$). The 95% confidence limits for TOBEC-estimated body fat were −7.37–2.96 g for 0 g estimated body fat, −1.04–8.82 g for 2 g estimated body fat, and 1.46–24.61 g for 5 g estimated body fat (Fig. 1B).

Several variables (% water of lean mass, body fat, % fat of live mass, feather mass, sex) were regressed against the residuals of the regression of TOBEC on lean mass in order to identify factors that affect the accuracy of TOBEC-estimated lean mass; none were correlated with the residuals ($P > 0.05$).

The contribution of TOBEC for predicting body fat was examined using multiple regression analysis, with body fat as the dependent variable and live body mass, TOBEC, and sex as independent variables. The model was significant ($F_{3,21} = 3.85$, $P = 0.024$) but explained only 36% of the variation in body fat. Live body mass ($P = 0.01$) and TOBEC ($P = 0.028$) both contributed significantly to explaining the variation in body fat, but sex did not ($P > 0.05$). However, live body mass was a better predictor of body fat than TOBEC, and live body mass and TOBEC together could explain less than half of the variation in body fat.

Average body mass and lean body mass of starlings used in the validation were normally distributed ($P > 0.05$, N = 63). However, body fat ($P = 0.011$) and % body fat ($P = 0.007$) were not distributed normally. Average body mass of adult males (88.5 g, SD = 3.23, N = 27) was greater than for adult females (79.4 g, SD = 5.04, N = 27; $t = -4.801$, df = 61, $P < 0.0005$). Average juvenile body mass (81.7 g, SD = 8.57, N = 9) was not different from average adult body mass (84.0 g, SD = 6.22, N = 54), but the sample size of juveniles was small. Body fat as a percent of live mass and total body mass were not related ($r^2 < 0.01$, $F_{1,50} = 0.47$, $P = 0.497$, N = 52, $b = 0.012$). Average % body fat of males (4.00%) and females (3.93%) were not different ($t = -0.276$, df = 50, $P = 0.784$). However, lean mass was greater for adult males (85.1 g, SD = 3.18, N = 25) than for adult females (76.3 g, SD = 4.28, N = 20; $t = 7.9$, df = 43, $P < 0.0005$).

The coefficient of variation for the six TOBEC measurements for each subject averaged 1.5% (SD = 1.269, range = 0.0–8.6%, N = 63). Eleven individuals were excluded from the validation because of high variance in % fat of extracted aliquots. The regression of TOBEC as a function of lean body mass was significant ($r^2 = 0.66$, $F_{1,50} = 97.2$, $P < 0.0005$, N = 52, $b = 1.97$). Removal of an outlier caused by an individual with wet plumage during TOBEC analysis increased the correlation ($r^2 = 0.75$, $F_{1,49} = 142.4$, $P < 0.0005$, N = 51, $b = 2.06$). TOBEC was related to

lean body mass by: TOBEC value = −58.143 + 2.063(lean mass). The average residual of the regression of TOBEC on lean mass was 6.03 TOBEC units (SD = 4.60, range = 0.01–19.93 TOBEC units, N = 51). The 95% confidence limits for TOBEC-predicted lean mass were 56.4–72.7 g for 65 g estimated lean mass, 72.3–87.7 g for 80 g estimated lean mass, and 87.3–103.5 g for 95 g estimated lean mass (Fig. 1C).

The regression of TOBEC-estimated body fat on solvent-extracted body fat was only marginally significant (r^2 = 0.084, $F_{1,49}$ = 4.456, P = 0.040, N = 51, b = 1.473) and body fat explained only 8% of the variation in TOBEC-estimated body fat. The 95% confidence limits for body fat estimated from TOBEC were −33.5–22.4 g for 0 g estimated body fat, −8.4–25.7 g for 4 g estimated body fat, and 2.9–101.6 g for 10 g estimated body fat (Fig. 1D). Feather mass, water mass, body fat, sex, % water of lean mass, and % body fat of live mass did not explain a significant portion of the variance in the residuals of the regression of TOBEC on lean mass ($P > 0.05$).

The multiple regression model with body fat as the dependent variable and live body mass, TOBEC, and sex as independent variables was significant ($F_{3,47}$ = 4.585, P = 0.007), but explained only 23% of the variation in body fat. Live body mass (P = 0.003) and TOBEC (P = 0.044) both contributed significantly to explaining variation in body fat, but sex did not ($P > 0.05$). As with House Sparrows, live body mass of starlings better predicted body fat than did TOBEC, and live body mass and TOBEC together could explain less than half of the variation in body fat.

DISCUSSION

TOBEC was highly correlated with lean mass in the two study species. However, estimates of lean mass from the SA-1 TOBEC analyzer were not sufficiently precise for estimation of body fat in either species. For House Sparrows, the average residual of the regression of TOBEC on lean body mass was 1.678 TOBEC units, which corresponds to 1.18 g of lean body mass. Average body fat was only 1.08 g (SD = 0.407, range = 0.42–2.26 g, N = 25), so the average error in TOBEC-predicted lean mass exceeded average fat reserves. For European Starlings, the average residual was 6.03 TOBEC units which corresponds to 2.92 g lean mass. Average body fat was 3.34 g (SD = 0.743, range = 2.05–5.20 g, N = 52). Consequently, a large change in fat reserves for either sparrows or starlings was not detectable using the SA-1 and the instrument was not precise enough for monitoring temporal variation in body fat in these two species. The large 95% confidence intervals for the estimation of lean mass or fat mass from TOBEC indicate the lack of precision of the SA-1 when used with small birds weighing less than 100 g.

Scott et al. (1991) developed a TOBEC calibration curve for European Starlings based on a sample of 10 individuals. The 95% confidence interval for TOBEC-predicted lean mass (80 g estimated lean mass) was ±2.5 g in that study, compared with ±7.7 g in the present study. Scott et al. (1991) obtained a smaller 95% confidence interval, at least in part, because they treated TOBEC as the dependent variable and lean mass as the independent variable in the regression model. This statistical approach results in smaller confidence intervals (inverse regression need not be used to calculate confidence intervals), but it violates the assumptions of linear regression. Intraspecific variation in TOBEC is primarily a function of variation in lean mass, not the reverse. Linear regression assumes that the independent variable (x) is measured without error and the dependent variable (y) is normally distributed for any fixed value of x (Sokal and Rohlf 1981:496). Lean mass can be measured with reasonable accuracy using proximate analysis techniques, but TOBEC values are subject to substantial error related to the subject's posture and position in the measurement chamber. Consequently, lean mass should be the independent variable and TOBEC the dependent variable.

Linear models best fit the relationship between TOBEC and lean mass for a single species, but a quadratic model best describes curves composed of several species (Walsberg 1988, Scott et al. 1991). A quadratic function fitted to the House Sparrow and European Starling data had an r^2 of 0.98 ($F_{2,83} = 2252$, $P < 0.0005$). TOBEC data for Northern Bobwhite (*Colinus virginianus*) (Roby 1991) were combined with House Sparrow and European Starling data to provide an even wider range of lean body mass. TOBEC was significantly correlated with lean mass, using a simple linear model ($r^2 = 0.95$, $F_{1,121} = 2589$, $P < 0.0005$), but a quadratic function provided a better fit ($r^2 = 0.996$, $F_{2,120} = 12{,}152$, $P < 0.0005$, Fig. 2). The quadratic prediction equation was: TOBEC value = $-2.152 + 0.084$(lean mass) + 0.018(lean mass)^2. However, predicting lean mass of a previously unvalidated species from such a multiple species quadratic curve is likely to result in large errors for two reasons. First, body shape varies considerably among bird species of similar mass, and this variability will influence TOBEC readings. Also, it violates the assumptions of regression (Sokal and Rohlf 1981) to use quadratic prediction equations derived from several species to predict lean mass of a species with a different lean mass. Data for each species are clustered and behave as a point defining the regression line. Fig. 2 illustrates how inaccurate previously derived quadratic prediction equations can be for estimating lean mass of other species. TOBEC should, therefore, be validated for each species being studied (or a closely-related species of similar body mass and shape) and a species-specific regression formulated.

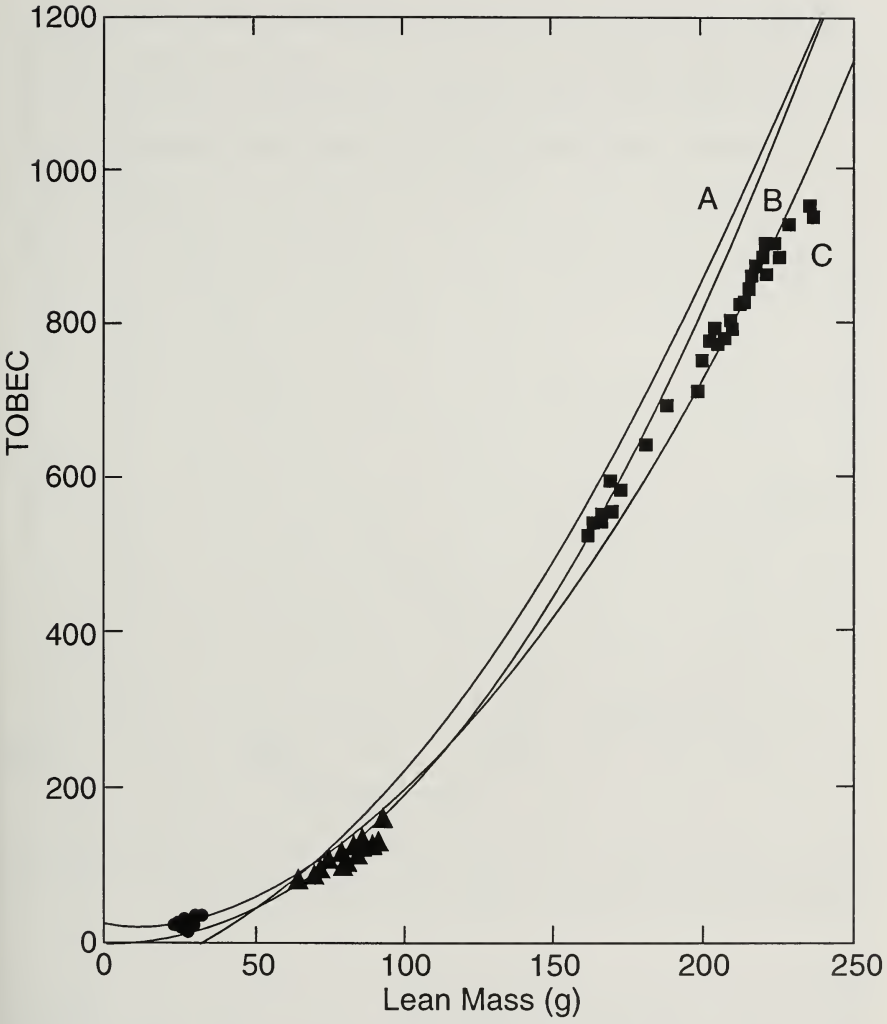

FIG. 2. Quadratic prediction curves of TOBEC vs lean mass derived by (A) Walsberg (1988), (B) Scott et al. (1991), and (C) this study. Circles represent House Sparrows (present study), triangles represent European Starlings (present study), and squares represent Northern Bobwhites (Roby 1991).

The slopes of the regression of TOBEC on lean mass increased with an increase in lean mass for House Sparrows (b = 1.43), European Starlings (b = 2.06), and Northern Bobwhite (b = 5.85). The trend of increased TOBEC as a function of increased subject size can best be described by a quadratic curve (Fig. 3). The curvilinear relationship between

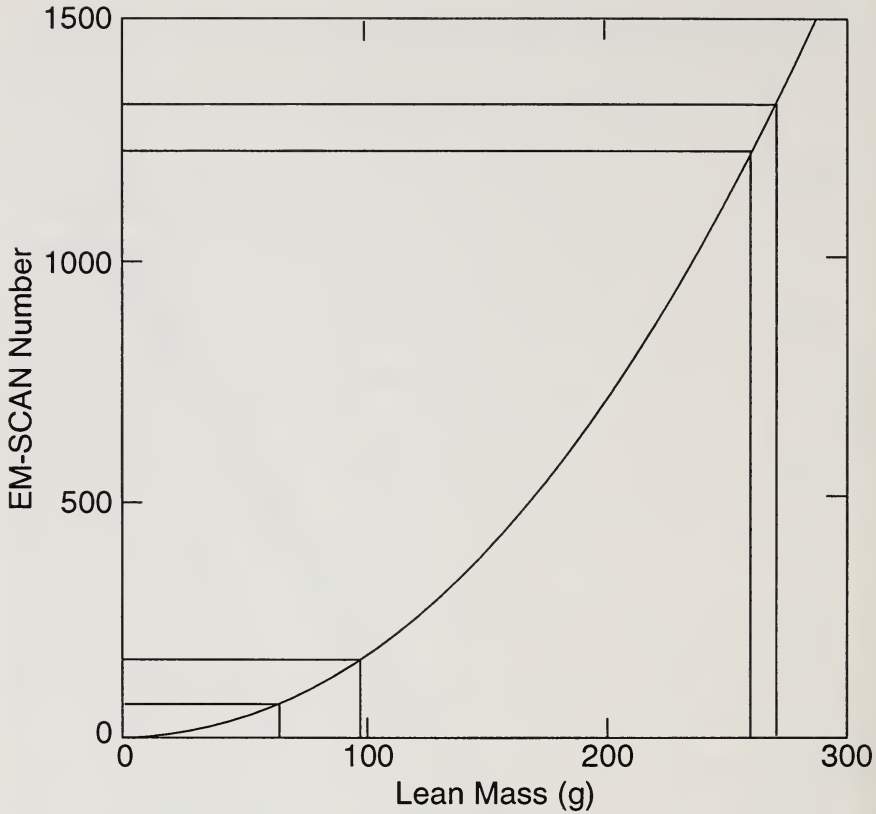

FIG. 3. Quadratic curve fitted to data on TOBEC as a function of lean mass for House Sparrows, European Starlings, and Northern Bobwhites. The upper pair of horizontal lines is separated by the same number of TOBEC units as the lower pair.

TOBEC and lean mass indicates that the SA-1 and SA-2 are less precise for determining lean mass of small birds, such as sparrows and starlings. Precision of the prediction equation would be lower for smaller species because TOBEC values correspond to a wider range of lean mass (Fig. 3). TOBEC values that fall high on the curve will correspond to a relatively narrow range of lean body mass; thus precision will be higher for large subjects. Scott et al. (1991) also found that prediction of lean mass was more affected by error associated with TOBEC value in birds weighing 40–60 g lean mass than larger birds weighing 150–200 g lean mass.

Measurements of a calibration standard varied as much as five TOBEC units from day-to-day. This drift is well within the limits established for proper functioning of the instrument (Em-Scan, Inc., pers. comm.). How-

ever, we can use this error rate to illustrate the instrument's lack of precision for measuring birds <100 g live mass. Using species-specific prediction equations, a change of five TOBEC units corresponds to a change in predicted lean mass of 0.85 g for bobwhite (Roby 1991), 2.42 g for European Starlings, and 3.51 g for House Sparrows. Consequently, a slight change in the accuracy of the TOBEC instrument associated with normal day-to-day variation in measurement of a calibration standard would be of little consequence when measuring a large subject (e.g., bobwhite), but important when measuring smaller subjects. Also, the converse indicates that a small change in lean mass is easily detectable in >200 g subject, but not in a subject <100 g.

This study demonstrates important constraints for using the SA-1 or SA-2 TOBEC analyzers for measuring small amounts of body fat in passerines and other small birds weighing less than about 100 g. Large changes in body fat (such as a doubling of fat reserves) of species the size of House Sparrows or European Starlings would not be detectable by the SA-1 or SA-2 due to the error in estimation of lean body mass from TOBEC. Despite these limitations, we think that TOBEC analysis is a promising technique for research that requires nondestructive measurement of body composition in live birds, particularly when temporal variation in body composition is considerable. Previous validations of the SA-1 and SA-2 indicate it is precise enough for measuring body composition in species approaching the maximum size that can be inserted in the measurement chamber (about 175–275 g body mass; Roby 1991). Precision of body fat estimates in smaller subjects would be correspondingly improved by using a smaller subject chamber equipped with a smaller coil. Development of new instruments with smaller and larger coil diameters than the SA-1 and SA-2 should extend the usefulness of this technique to include the study of a much wider range of subject sizes. A new generation of Small Animal Body Composition Analyzers (SA-3000) are currently being developed that will include a range of measurement chamber sizes (Em-Scan, Inc. 1993). The SA-3000 could make the TOBEC technique more versatile and potentially meet the need for a simple, accurate, and nondestructive method for measuring body composition of birds weighing 10–3000 g.

ACKNOWLEDGMENTS

We thank M. Eichholz, J. Byrd, A. Nelson, B. Richards, and E. Shaffner for valuable field assistance. Earlier drafts of this paper were improved by comments provided by G. E. Walsberg, T. V. Dailey, and an anonymous reviewer. Support for this study was provided by the Cooperative Wildlife Research Laboratory and the Office of Research Development and Administration, Southern Illinois Univ.

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Wilson Bull., 107(2), 1995, pp. 317–327

AVIAN PREDATION AT PENGUIN COLONIES ON KING GEORGE ISLAND, ANTARCTICA

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Abstract.—Predation at seven colonies that varied in size from 10 to hundreds of breeding pairs of Adelie (*Pygoscelis adeliae*) and Gentoo (*P. papua*) penguins was observed from a blind at King George Island, Antarctic Peninsula, from 21 Dec. 1993 to 3 Feb. 1994. We observed the colonies for 96 h to record foraging by Brown Skuas (*Catharacta lonnbergi*), Kelp Gulls (*Larus dominicanus*), and Giant Petrels (*Macronectes giganteus*) during the early chick through creche phase of the penguin breeding cycle. Activity rates by predators varied little with time of day or time of season for skuas and petrels. Kelp Gulls, however, showed significant variation in rates with time of season. Total activity and search rates were significantly higher for each predator species at larger versus smaller colonies. In addition, attempted predation and predation by skuas on penguin chicks were significantly higher, and from 4.1–7.9× more frequent, at colony edges rather than the center. Larger colonies probably receive greater attention by predators because of the larger number of prey, and by their greater circumference and edge area. Low breeding success by penguins in small colonies appeared to be partially attributed to predation losses, although predation rates were low. Penguin reproductive success may be significantly influenced by colony size and by the number and kinds of predators attending them. *Received 8 Sept. 1994, accepted 15 Nov. 1994.*

Predation at breeding colonies has received a great deal of attention by ornithologists interested in the evolution and adaptive significance of coloniality (e.g., Wittenberger and Hunt 1985, Kharitonov and Siegel-Causey 1988). In general, the number of predators and predation rates increase with colony size, but the proportion of prey killed usually decreases. This pattern suggests that large colonies provide greater protection for prey offspring due to the swamping effect of prey numbers on the predator. However, some studies have produced divergent results and indicate that the predator-prey relationship at colonies is complex and varies in different systems in relation to the number and kind of predators and the size and age of the colony (Davis 1982, Raveling 1989, Hunter 1991, Szep and Barta 1992). To test the hypothesis that larger rather than smaller colonies provide greater protection to penguin chicks, we examined predator activities at colonies of various sizes of Adelie (*Pygoscelis adeliae*) and Gentoo (*P. papua*) penguins in Antarctica. We determined activity rates in relation to time of day, time of season, and colony size and examined the effect of predation on reproductive success of penguins

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in small and large colonies. We compare our results with other studies to explain the predator-prey relationship in the Antarctic system.

METHODS

This study site is located at Llano Point on the western shore of Admiralty Bay, King George Island (Lat. 62°10′S, 58°30′W), South Shetland Islands (see Trivelpiece et al. 1990 for description of the study area). At Llano Point, colonies of Adelie and Gentoo Penguins have been censused and monitored for reproductive success each year since 1980. During the 1993/1994 breeding season, we estimated the breeding populations of these species at 6100 Adelie and 2200 Gentoo pairs. These estimates are based on nest counts conducted at peak egg laying in early and mid-November, respectively. Fledging success was based on chick counts completed in January and reproductive success, measured as chicks fledged per breeding pair, was calculated for each colony by dividing the number of chicks fledged by the number of nests. In addition, ten pairs of Brown Skuas (*Catharacta lonnbergi*), 120 pairs of Southern Giant Petrels (*Macronectes giganteus*), and approximately 20 Kelp Gulls (*Larus dominicanus*) comprised of 5–6 breeding pairs plus subadults and non-breeders occurred near these colonies.

We observed seven colonies of Adelie and Gentoo penguins from a blind between 21 Dec. 1993 and 3 Feb. 1994. Activities of Brown Skuas, Kelp Gulls, and Giant Petrels were recorded during 2-h observation periods that were sequentially alternated between 06:00 to 20:00 h each day. We continuously scanned the colonies during each period and recorded searches, attempted predation, predation, and scavenging on penguin eggs and chicks by these predators. Searches were recorded when birds hovered or flew low and circled slowly over the colonies or walked near the colony edges; a rapid, direct flight over the colonies was not considered a search. Attempted predation occurred when birds took and lost, or attempted to take, penguin eggs or chicks. Predation was recorded when a predator successfully removed a live chick or egg from the colony or creche and it died as a result of this removal. Scavenging occurred when birds began feeding on carcasses or spilled krill in or near the colonies. We recorded the location of predation and attempted predation events in the colony as either having occurred at the periphery (within three nests of the edge, see Ainley et al. 1983) or center (beyond three nests from the edge) of the colony. Local weather conditions also were recorded during each observation period; however, the relatively mild season in 1993/1994 precluded an analysis of predation rates with variations in weather conditions.

Activity rates for each predator species were calculated by dividing the number of events recorded by the number of hours of observation. These rates were determined for each species, and not individual predators, by time of day, time of season (divided into 5-day intervals that included at least 8 h of observations each), and colony. For Brown Skuas and Giant Petrels, we divided these rates into three categories: total activities (searches, attempts, predation and scavenging), searches and predation. We did not observe Kelp Gulls preying on guarded penguin eggs or chicks, but they frequently scavenged spilled krill from penguin feedings in and near the colonies. Thus, for Kelp Gulls, we substituted scavenging for predation rates. Data were analyzed using Chi-square goodness of fit, linear regression, and Spearman's Coefficient.

RESULTS

We completed 96 h of observations at the colonies. Brown Skuas and Giant Petrels had higher total activity rates than Kelp Gulls during the

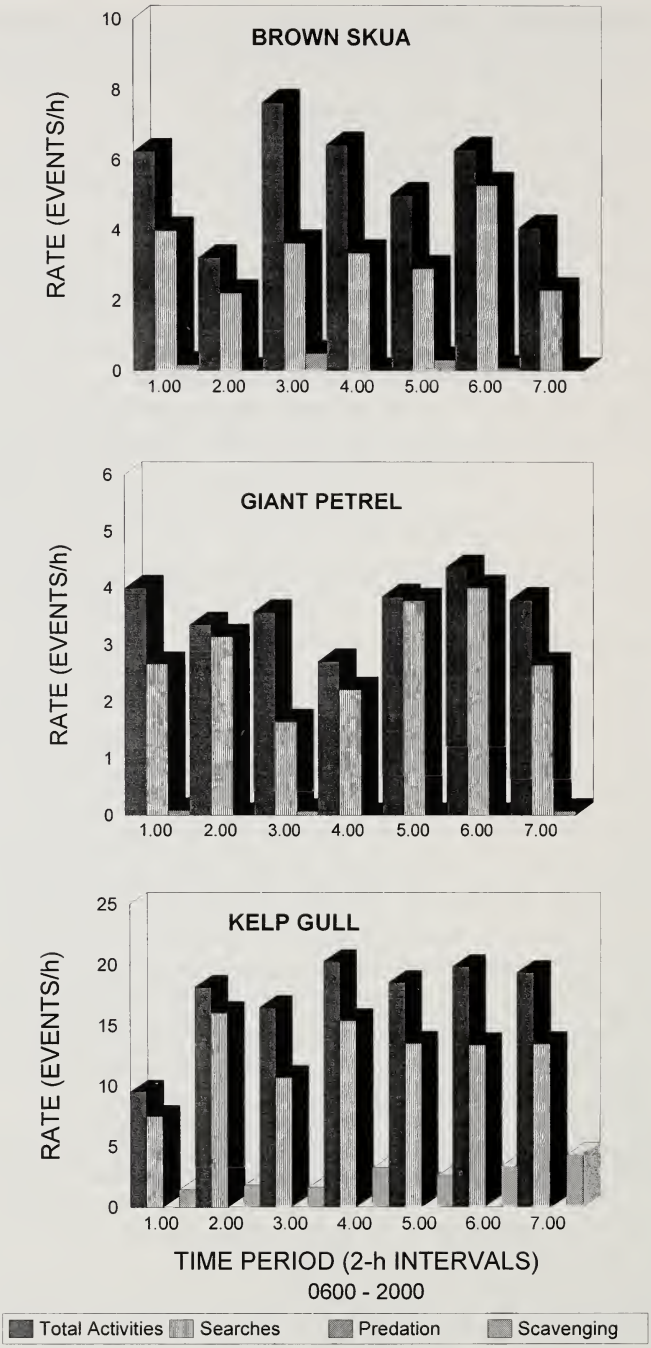
early morning (06:00–08:00 h), but there was no significant diurnal pattern for each species ($\chi^2 < 4.70$, df = 6, $P > 0.5$; Fig. 1). Predation rates were highest for skuas in the late morning and mid-afternoon and for petrels in the early morning and early evening. Kelp Gulls scavenged most frequently in the afternoon and early evening. Although these rates did not vary significantly, they suggest that these predators may partition their respective activities throughout the day.

Although there was a gradual decline in skua, and an increase in Giant Petrel, total activity and search rates throughout the season, no activity by each of these predators varied significantly with time of season (Fig. 2). However, there was a noticeable but non-significant increase in Giant Petrel total activity coincident with the hatching of the first Giant Petrel chicks, and a decrease in skua activities after peak creche (Fig. 2).

Total activities and searches by Kelp Gulls varied significantly ($\chi^2 > 29.3$; df = 8; $P < 0.05$) with time of season and were highest during period 6 (15–19 Jan.; Fig. 2). Except for scavenging which did not vary with time of season ($\chi^2 = 12.57$; df = 8; $P < 0.1$), all activities by this species declined steadily after period 6. Scavenging rates declined markedly in period 7 (20–24 Jan.), increased in period 8 (25–29 Jan.), but declined again thereafter.

All activities by each predator species were positively correlated with colony size (Spearman's Coefficient $R > 0.82$, N = 7, $P < 0.05$; Table 1). Search and scavenging rates by Kelp Gulls also were correlated positively with colony size ($R = 0.86$, $P < 0.05$). Predation rates by skuas, however, were not correlated with colony size ($R = 0.64$, $P < 0.11$), and predation rates by Giant Petrels were too low for statistical analysis. Predation events were rare but occurred most often at the larger colonies (Table 1). Small colonies were rarely visited by predators. Predation and attempted predation by skuas on penguin chicks was significantly higher and from 4.1–7.9× more frequent at the periphery of the colony than in the center ($\chi^2 = 27.6$, df = 1, $P < 0.005$; Fig. 3). Moreover, these activities were slightly, but not significantly, higher from the ground than from the air. All predation and attempted predation by Giant Petrels occurred from the ground and at the edge of creches.

We observed a non-significant increase in reproductive success with colony size in Gentoo Penguins ($R^2 = 0.53$; df = 5; $P < 0.1$). Reproductive success increased to a maximum of 1.3 chicks per pair for colonies with 34 or more nests; however, colony 9 with only 10 nests had no chicks surviving (Table 1). Although we did not witness predation at this colony, we did observe the same pair of skuas attempting to take chicks on several occasions, and we suspect that their efforts may have


BROWN SKUA
RATE (EVENTS/h)
10
8
6
4
2
0
1.00
2.00
3.00
4.00
5.00
6.00
7.00
GIANT PETREL
RATE (EVENTS/h)
6
5
4
3
2
1
0
1.00
2.00
3.00
4.00
5.00
6.00
7.00
KELP GULL
RATE (EVENTS/h)
25
20
15
10
5
0
1.00
2.00
3.00
4.00
5.00
6.00
7.00
TIME PERIOD (2-h INTERVALS)
0600 - 2000
Total Activities
Searches
Predation
Scavenging

removed many of the chicks from this colony. No pattern was observed with Adelie Penguin reproductive success and colony size.

DISCUSSION

A potential problem in these analyses is the attribution of most skua activities at the colonies to three pairs of breeding birds (recognized by their color bands) that held feeding territories in the study area. Although other skuas occasionally visited the colonies, these three pairs may bias the data toward individually learned behavior. Moreover, our study was of short duration and limited to the chick period of the penguin breeding cycle.

During our study, the weather was consistently mild, and we could not address the effect of severe weather conditions on predator activities. Young (1994) reported higher predation by South Polar Skuas (*Catharacta maccormicki*) on windy or stormy days when the adult penguins may be distracted or oriented in one direction, thereby facilitating prey capture. He also found variation in predation rates in relation to ice conditions and marine productivity in Antarctica. Similarly, predation of Common Murres (*Uria aalge*) and Brandt's Cormorants (*Phalacrocorax penicillatus*) by Western Gulls (*Larus occidentalis*) was higher in poor food years, causing additional constraint on the breeding effort by murres during those years (Spear 1993). We suspect predation rates will vary annually at King George Island because of these factors, but additional data are needed.

We found no variation in Brown Skua and Giant Petrel activity rates with time of day or season. Searches were the most common predator activity recorded during all observation periods. The ratio of searches to predation events was high, similar to those reported in other studies of South Polar Skua predation at Adelie Penguin colonies (Müller-Schwarze and Müller-Schwarze 1977, Young 1994). Müller-Schwarze and Müller-Schwarze (1977) suggested that frequent searches by predators at these colonies may facilitate predation by acclimating penguins to their presence, thereby causing them to be less alert. Equally possible is that skuas search the colonies continuously to locate vulnerable prey or to assess prey for future targets. We observed skuas returning to the same nest

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FIG. 1. Activity rates of predators with time of day at King George Island. Each time period represents a 2-h observational interval between 06:00 to 20:00 h. For each predator and each time period, activity rates are graphed for total activities and separately for searches and predation only. Scavenging rates, and not predation, are shown for Kelp Gulls only in the lower graph.

TOTAL ACTIVITY RATES
1st petrel chick
peak creche
RATE (EVENTS/h)
SEARCH RATES
RATE (EVENTS/h)
SCAVENGING
PREDATION
RATE (EVENTS/h)
FIVE-DAY OBSERVATION INTERVALS
21 Dec. 1993 - 3 Feb. 1994
Brown Skua
Giant Petrel
Kelp Gull

repeatedly until the prey was successfully taken. These nests usually contained small chicks or were more vulnerable to predation at the periphery of the colony.

Two species of Giant Petrels (*Macronectes giganteus* and *M. halli*) prey heavily on penguins, but have received less attention than skuas as their breeding range overlaps with penguins only in the Antarctic Peninsula and sub-Antarctic regions. Previous to our study, only Hunter (1991) has determined predation rates by Giant Petrels on penguins and at colonies of different sizes. Our observed predation rates by Brown Skuas and Giant Petrels are comparable to those reported for these species on King Penguins (*Aptenodytes patagonicus*) at Marion Island (Hunter 1991), and for South Polar Skuas on Adelie Penguins at Cape Crozier (Müller-Schwarze and Müller-Schwarze 1977) and Cape Bird (Davis 1982). These studies were based on systematic observations of penguins throughout the breeding period.

Our results agree with these studies in that predation was highest at larger colonies, although not significantly so. Davis (1982) found a significant and negative correlation between size of Adelie creches and the proportion of chicks depredated. Although the number of chicks lost was greatest at the largest creche, the proportion was smallest. He also attributed differences in reproductive success at penguin colonies to differential predation by skuas; colonies where the greatest number of South Polar Skuas foraged had the lowest reproductive success. We did not observe this pattern in our colonies where each had no more than two overlapping skua territories; Davis (1982) recorded from two to seven skua territories at each of his colonies.

Hunter (1991) counted corpses of chicks at colonies of King Penguins depredated by Brown Skuas and Giant Petrels. Similar to our results, he found daily predation rates determined from these counts to increase with colony size. He also found more corpses at the larger colonies, but the proportion of chicks lost (calculated from data in his Table 6) increased with size in some colonies (e.g., 11.5% in Kildalkey Bay A-D with 1457 chicks versus 19.8% at Prinsloomeer with 1848 chicks), the reverse pattern from that of Davis (1982). This difference may have been due to the greater number and diversity of predators at Marion Island (3 species) compared to Cape Bird (1 species). If so, variation in reproductive success

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FIG. 2. Activity rates of predators with time of season at King George Island for total activities (top), searches (middle), and predation (skuas and petrels) or scavenging (Kelp Gulls; bottom). The breeding season is divided into nine 5-day intervals, with from 8–14 hours of observations each, beginning 21 Dec. 1993.

TABLE 1

TOTAL ACTIVITY AND PREDATION RATES FOR BROWN SKUAS AND GIANT PETRELS AT THE SEVEN OBSERVATION COLONIES OF ADELIE (A) AND GENTOO (G) PENGUINS ON KING GEORGE ISLAND, ANTARCTICA, 21 DEC. 1993–3 FEB. 1994

Colony/species		No. nests	No. chicks	Chicks per pair	No. chicks seen killed	Skua total rates	Skua predation rates	Giant Petrel total rates	Giant Petrel predation rates
1	A	not counted	not counted	1.30[a]	11	4.21	0.083	2.92	0.031
4	A	36	39	1.08	2	0.15	0.021	0.052	0
5	A/G	71/45[b]	59/50[b]	0.83/1.11[b]	0	0.34	0	0.41	0
6	G	56	70	1.25	1	0.12	0.010	0.052	0
7	G	19	17	0.90	0	0	0	0	0
8	G	34	43	1.27	5	0.24	0.052	0.052	0
9	G	10	0	0	0	0.083	0	0.010	0

[a] Based on a monitored sample of 40 nests.

[b] Refers to Adelie/Gentoo penguins, respectively, that both bred in this colony. Data on colony size, number of chicks counted at fledging and reproductive success measured by the number of chicks fledged per pair at each colony also are given.

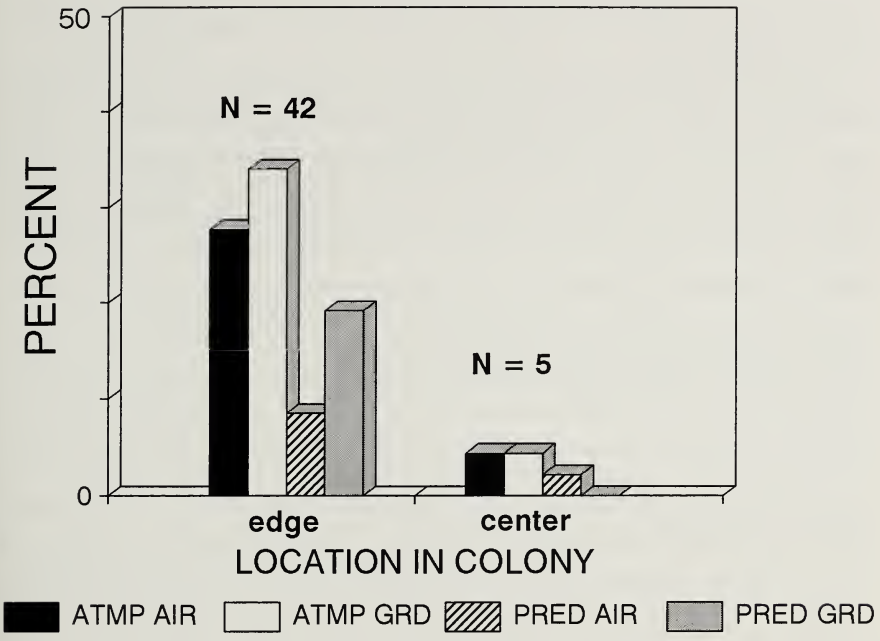

FIG. 3. Percent of total (N = 47) attempted predation and predation events on penguin chicks by Brown Skuas that were recorded from the air or ground and at colony edges or centers at King George Island.

by penguins of the same species, but at different colonies, may be due in part to the number and kinds of predators that attend them.

Increased predation with colony size is not difficult to explain. Larger colonies have a greater number, but small proportion, of nests on the periphery than smaller colonies (if their shape remains the same), and there is a greater variety of prey ages and sizes. Thus, predators should spend more time searching at large colonies where there is a better chance at finding a vulnerable target. Our findings that predation and attempted predation occur more frequently at colony edges supports this hypothesis. Spear (1993) also found higher predation by Western Gulls at the periphery of Common Murre colonies. However, colonial behavior is not adaptive as a means of reducing predation unless the proportion of prey taken by predators decreases with colony size. Our data on reproductive success with colony size also support this hypothesis. In addition, lower reproductive success in Adelie Penguin colonies may be due to a greater percentage of young or inexperienced breeders that may occur at the periphery of these colonies (Ainley et al. 1983). Small Gentoo Penguin colonies may be similarly biased with young breeders and this factor may account

for the lower success rates that we observed in colonies with less than 34 nests (Table 1).

Colonial-breeding penguins and their avian predators in the Antarctic represent a system in which both predator and prey are forced to co-exist due to lack of ice-free areas for breeding. One major predator, the South Polar Skua, often holds feeding territories that include penguin colonies but does not rely on this resource for successful breeding (Young 1994). Other studies, however, have indicated that both South Polar and Brown skuas with feeding territories have significantly higher reproductive success than pairs without feeding territories (Trillmich 1978, Trivelpiece et al. 1980, Trivelpiece and Volkman 1982, Pietz 1987, Young 1994). Spear (1993) had a similar finding for Western Gulls that held feeding territories within colonies of Common Murres and Brandt's Cormorants. Thus, life history strategy of skuas appears to benefit from the relationship whether it is obligate or opportunistic. For penguins, large colonies appear to be the best strategy for maximum reproductive success, but only for nests not located on the periphery. Our study indicates that the number and kinds of predators are important determinants in penguin reproductive success. Other studies suggest that variations in annual marine productivity also may be important (Spear 1993, Young 1994). Reproductive success in penguins should be interpreted in light of all these variables, especially when the impact of human disturbances or other unusual events are investigated.

ACKNOWLEDGMENTS

We thank R. Dilling and S. Klock for assistance in the field. Useful suggestions and discussions were provided by W. Fraser, M. Moulton, and S. Trivelpiece; M. Stiger assisted with graphics. The manuscript was improved by comments from G. Miller and an anonymous reviewer. This research was funded by NSF Grant DPP-9121952 to W. and S. Trivelpiece with supplemental funding to S. Emslie.

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Wilson Bull., 107(2), 1995, pp. 328–337

HATCHING, GROWTH, AND MORTALITY OF MAGNIFICENT FRIGATEBIRD CHICKS IN SOUTHERN BAJA CALIFORNIA

Roberto Carmona, Juan Guzmán, and Juan F. Elorduy

Abstract.—We studied growth and development of chicks of the Magnificent Frigatebird (*Fregata magnificens*) in 1985, 1986, and 1988 at a colony on Isla Santa Margarita, Baja California Sur, México. Hatching peaked at weeks 7, 12, 17.5, and 23.3 of the calendar year. Hatching frequencies around each peak were distributed normally. Growth was analyzed using Richards' model. Total length had the lowest growth rate and mass the highest. The asymptote for mass was reached before 150 days, as was the asymptote for culmen; the asymptotes for wing and wingspan were reached later. Chick mortality, recorded over a six-month period, was considered to be low (46%). During the same period there was 90% replacement and new occupation of nests, which resulted in temporal and spatial clustering of the clutches laid during the season. *Received 16 May 1994, accepted 1 Dec. 1994.*

Long-lived seabirds tend to have reduced clutch sizes and prolonged breeding seasons (Nelson 1979). The Magnificent Frigatebird (*Fregata magnificens*) represents an extreme case of this trend, having a clutch of one egg and a period of approximately 21 months from egg-laying to postfledging (Diamond 1972, 1973, 1975; Nelson 1975, 1979). Stonehouse and Stonehouse (1963) and Nelson (1967) hypothesized that females breed only biennially, whereas the males breed every year. From the eleventh week of chick's age males abandon both nest and colony (Moreno and Carmona 1988), so prefledging and postfledging feeding of the chick is fully assumed by the females. Frigatebird chicks are altricial and require about six months to fledge (Diamond 1973; Moreno and Carmona 1988). This prolonged care period produces a protracted reproductive season; in fact, Nelson (1967), Diamond (1972, 1973, 1975) and Kepler (1977) reported extended breeding in this frigatebird species with one to two annual peaks in laying in colonies located in tropical regions. Growth patterns in frigatebirds have received little attention, and the reports available (Diamond 1973, Nelson 1975) only present polynomial curves of actual data on mass, wing, and bill. In this paper, the timing of hatching, egg and chick mortality and chick growth are analyzed.

MATERIALS AND METHODS

We measured frigatebirds from May to October 1985, January to September 1986, and April to September 1988 at colony in the mangrove forest "Las Tijeras" at the southeast

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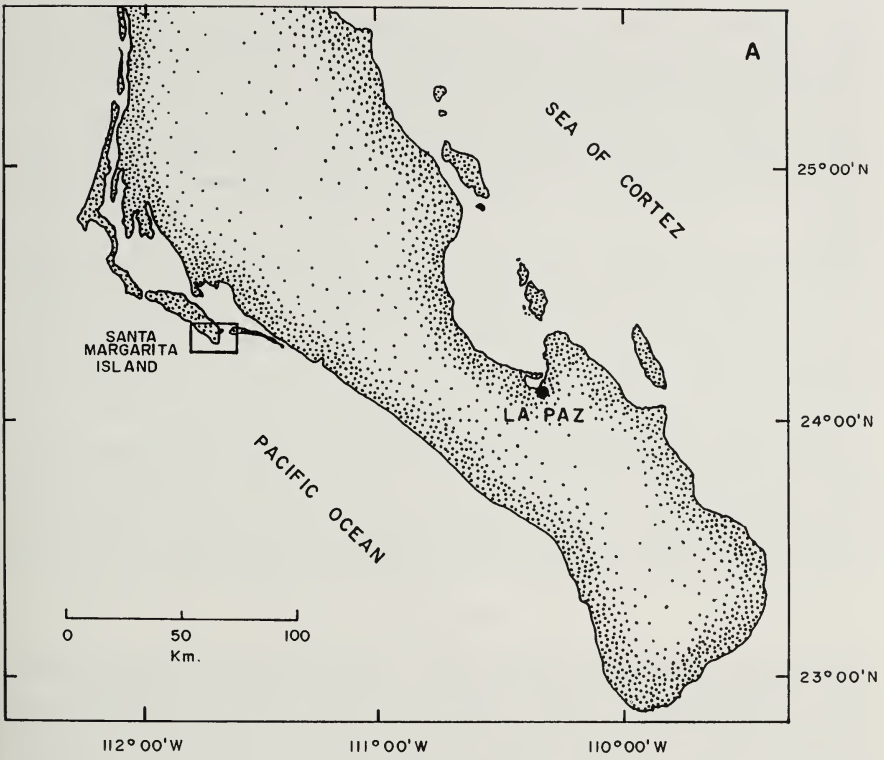


FIG. 1. Location of the Magnificent Frigatebird colony at "Las Tijeras" on Isla Santa Margarita.

end of Isla Santa Margarita (24°25'N, 111°07'W) on the west coast of Baja California Sur, México (Fig. 1). The mangrove forest covered an area of 0.8 km^2 surrounding a tidal lagoon approximately 500 m long and 50 m wide. The mangrove species were red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*). The canopy of the latter reached up to 5 m, covered about 22.8% of all mangrove areas, and was the preferred nesting substrate of the frigatebirds. Some nests were also built in red mangrove. The fragility of the mangrove branches presented a serious sampling problem, being a source of risk both for the chick to be captured and the researcher.

The hatching period was estimated by back calculation from a sample of 327 measurements of culmens taken randomly in the colony during three visits made in 1988 (April, June, and September). From the total sample, there were 35 data points on the size of culmens at hatching with their respective hatching dates, necessary for the back-calculation of hatching dates. The 327 back-calculated dates of hatching were grouped by weeks and analyzed for the presence of distinct modes by the Bhattacharya (1967) method. This is a statistical technique that separates into different gaussian (normal) components a polymodal frequency distribution.

For growth studies, we selected eight chicks in 1985 and 27 chicks in 1986. We measured the chicks every four days between hatching and fledging, which occurred at about five

months of age. We measured culmen, wing, wingspan, total length, with a measuring tape to the nearest 1 mm and culmen with vernier calipers to the nearest 0.1 mm. We measured mass with portable weight gauges. Precision was ±1 g up to 100 g; ±2 g from 101 to 300 g; ±10 g from 501 to 1000 g and ±50 g over 1000 g total mass.

We analyzed growth using Richards' sigmoid growth model (Richards 1959) and an iterative nonlinear regression technique (Marquardt 1963) and Statistical Graphics System 2.1. The curves derived from this model can be adequately interpreted from a biological point of view, i.e., by taking into account both physiological and ecological factors affecting growth.

The growth data collected in 1985 and 1986 were processed separately, and the resulting parameter estimates of asymptotic length (L) and mass (W), growth rate (K), and time to inflection of the curve (t_i) were tested for differences in slopes for the regressions (Student's *t*-test) and covariance analysis (*F* Fisher Test) for the homogeneity in the regression data (Steel and Torrie 1981). These showed there were no significant differences between years ($P < 0.001$ for the *t*-test with 70 degrees of freedom, and $P < 0.05$ for the *F*-test with 2, 70 degrees of freedom). Consequently, the two years' data sets were pooled.

To study chick and egg mortality, an area of approximately 300 m containing 90 active nests was selected in 1986. These nests were at a different location from the ones where growth studies had been conducted. The area was visited once a week over six months, and the number of new nests and their contents and those that had disappeared were recorded each time, taking extreme care to cause the least disturbance to the chicks.

RESULTS

Hatching.—The dates of hatching, as back-calculated from the 1988 data, were grouped by weeks, using the rationale that the standard error of the predicted curve for culmen length is about 3.5 days. The hatching dates showed four modes (Fig. 2A) that resulted in four distinct normal distributions, as tested with χ^2 tests of normality at a confidence level of 95%, with means at 7.05, 11.92, 17.45, and 23.33 weeks of the year, respectively, and standard deviations of 1.5, 1.45, 2.03 and 2.08 weeks, respectively (Fig. 2B). Moreover, a test of equality of the means was conducted, showing each peak as distinct from the other three, with their maxima separated by 5, 5.5 an 6 weeks, respectively.

Growth.—The pooled values for each parameter and structure (Table 1) were either identical to the 1986 values or extremely close (except for wing), which can be explained by the larger sample size in 1986. In all cases, the variance explained by the model (r^2) was very high. The average of data collected every four days (1985 and 1986), and the corresponding fitted curves, were characterized by a sudden variability of the means at about 100 days (Fig. 3). This variability, at least partially, can be attributed to sampling difficulties and to a decrease in sample size. The variability for mass gives, for example, a poorer fit to the model ($r = 0.96$). After 90 days, the handling of the chicks became rather laborious, and all individuals could not always be captured. The calculated curves were transformed to percentages of the asymptote of each mea-

surement. This puts the growth pattern of each structure in relative numbers so they can be compared to each other, and the growth pattern understood as a whole. Fig. 3B shows the following general characteristics (1) At hatching the size of wing, wingspan, and mass are relatively smaller but culmen and total length are relatively larger; (2) As expected, wing and wingspan growth are alike and their growth rates are similar to that of the culmen; (3) Total length had the lowest growth rate, and that of mass had the highest; and (4) The asymptote for mass (W) was reached before 150 days and the asymptote for culmen at 150 days. The structure that took longest to reach the asymptotic value was total length.

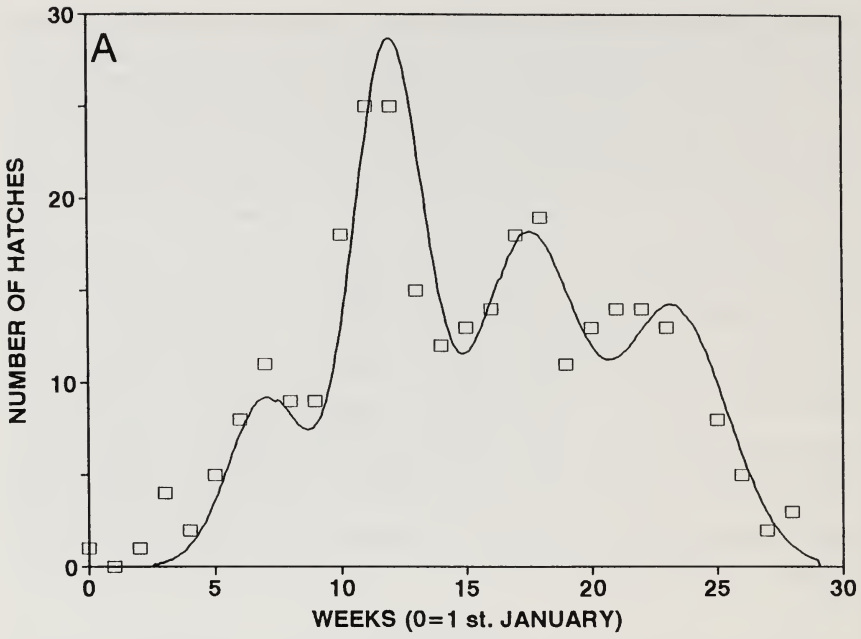
Mortality.—Chick mortality in the 90 original nests selected for monitoring, was 46% (Fig. 4). The highest mortality took place in April. As chicks died, new active nests appeared, sometimes built on top of abandoned ones. These new nests appeared mainly in March. After the last week of April, no new nests were observed. Mortality of chicks from new nests was only 30%, lower than that for the original group of 90 nests. The largest number of nests at one time was during the last week of March and first half of April.

DISCUSSION

The presence of four hatching peaks confirms the observation by Diamond (1973) that there were at least two laying peaks in Barbuda. The differences between Barbuda and Santa Margarita are probably due to differences in latitude and food availability, although the gross analysis made by Diamond may be another important reason for this difference.

Much usable space, occupied by young birds from the preceding breeding season, progressively became available by the start of the second laying period (about six weeks later than the first one). Once this second wave of reproduction was established, nesting space must have been near saturation (the highest peak recorded). This could explain why the third wave had a higher standard deviation (less synchronous) than the two preceding waves. The new pairs became established gradually as the males from the preceding groups abandoned the colony.

Nevertheless, the third batch had the higher number of chicks measured. The second and third laying groups were the main ones. If we consider there had been mortality of chicks from the three previous hatching waves (which makes the parents leave the nest), the fledglings from the first wave were already leaving, and the males from the second breeding group were abandoning their nests, the availability of space for nesting for the fourth group would have been at the same level as for the end of the second laying period. This could explain the similarity of the standard deviations between the third and fourth groups. The peak frequency


A
NUMBER OF HATCHES
WEEKS (0=1 st. JANUARY)
0
10
20
30
0
5
10
15
20
25
30

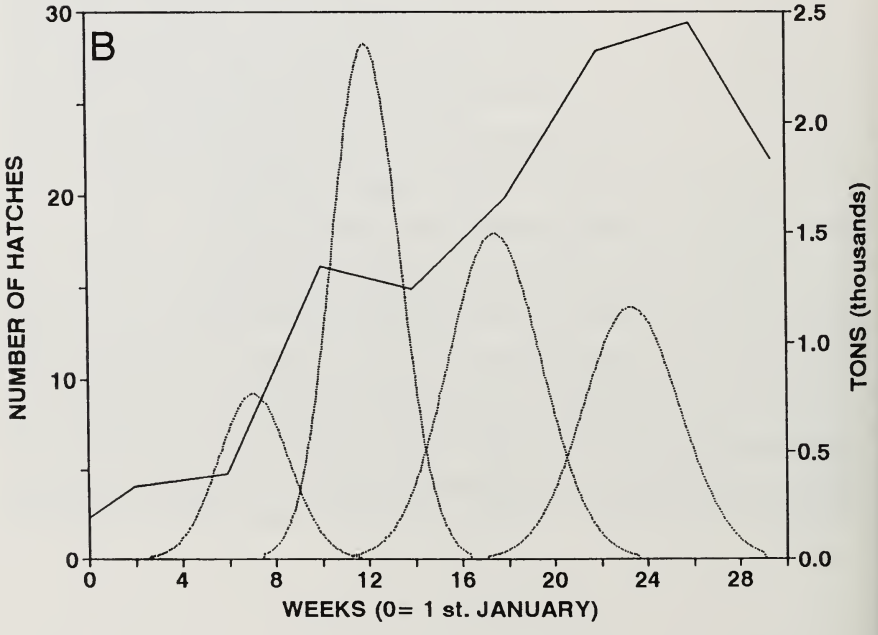

B
NUMBER OF HATCHES
TONS (thousands)
WEEKS (0= 1 st. JANUARY)
0
10
20
30
0.0
0.5
1.0
1.5
2.0
2.5
0
4
8
12
16
20
24
28

TABLE 1
PARAMETERS OF THE RICHARD'S CURVE[a]

Structure	Asymptote	K[a]	t_i[b] (days)	r^2[c]
Culmen	111.49	0.037	37.17	0.9864
Wing	1007.24	0.040	73.61	0.9910
Wing span	2077.50	0.041	70.11	0.9862
Total length	942.14	0.026	56.54	0.9877
Mass	1341.08	0.055	47.47	0.9609

[a] Pooled sample (1985 and 1986). Units of the asymptote in mm, except mass (g).
[b] Growth rate.
[c] t_i = Time to inflection of the curve.
[d] Variance explained by the regression model.

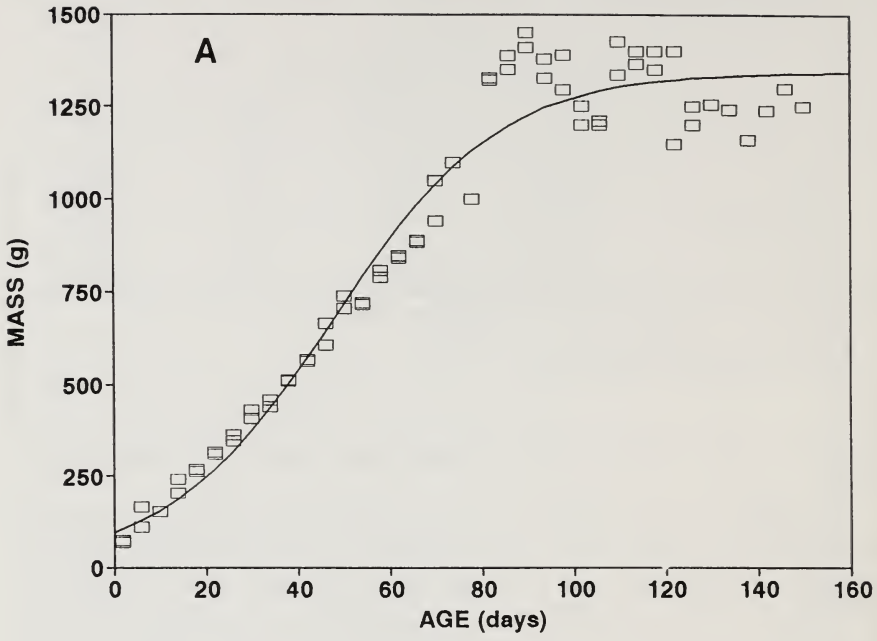
of only 15 also indicates that the breeding season was ending by that time.

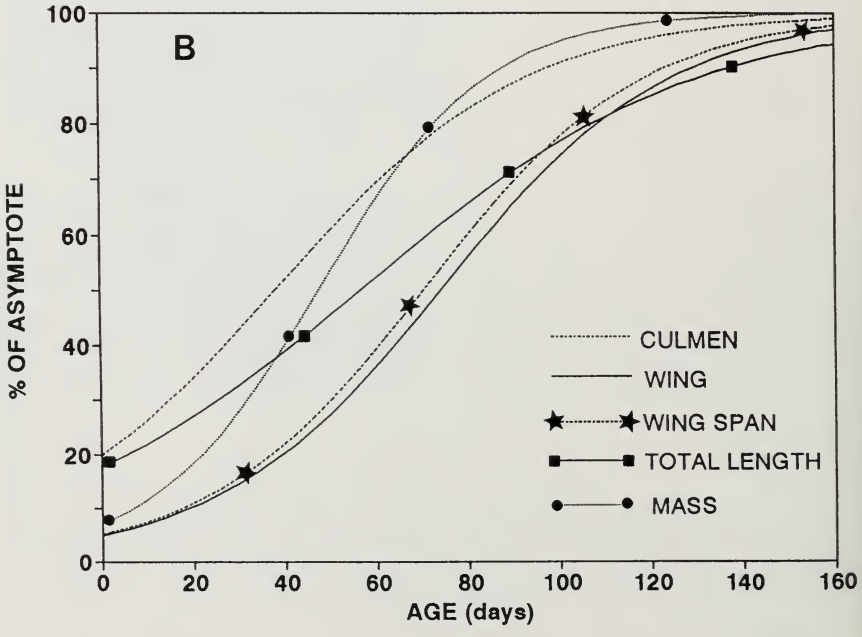
The parents do not remain on the nest during all of the growth period. Chicks are left alone 50% of the daylight hours after the first six weeks (an age at which they are able to defend themselves and the space immediately contiguous to the nest). As the chick grows, parents gradually travel farther and for longer periods while searching for food. Finally, adult males abandon the nest at the eleventh week after hatching (Moreno and Carmona 1988). We have observed that the space defended by a six-week-old chick was smaller than the one defended by its parents. We can assume the pressure on the territory next to an established nest decreases, allowing new males to attempt to establish their courting territories in the area. By the time of the third and fourth laying periods, the males of the first and second periods have already left, again giving more usable space for the establishment of new nests.

The availability of prey may be another factor explaining the overall seasonality of Magnificent Frigatebird breeding in the area. The most abundant component of the chick's diet, observed from regurgitates, was the "sardine" type group (Moreno and Carmona 1988). Frigatebirds in this area fish by sight for surface fish comprising a group of four clupeid and one scombroid species. The commercial fishermen also fish by sight so "sardine" captures are a good indicator of abundance of available prey.

←

FIG. 2. (A) Number of hatches per week, as backcalculated from culmen lengths (squares), and theoretical distribution of hatches adjusted for each peak (line). (B) Normal distributions based on data in figure 2A (light lines), and "sardine" captures for the year 1988 (heavy line), plotted as an indicator of the abundance of food.


A
MASS (g)
1500
1250
1000
750
500
250
0
0
20
40
60
80
100
120
140
160
AGE (days)


B
% OF ASYMPTOTE
100
80
60
40
20
0
0
20
40
60
80
100
120
140
160
AGE (days)
CULMEN
WING
WING SPAN
TOTAL LENGTH
MASS

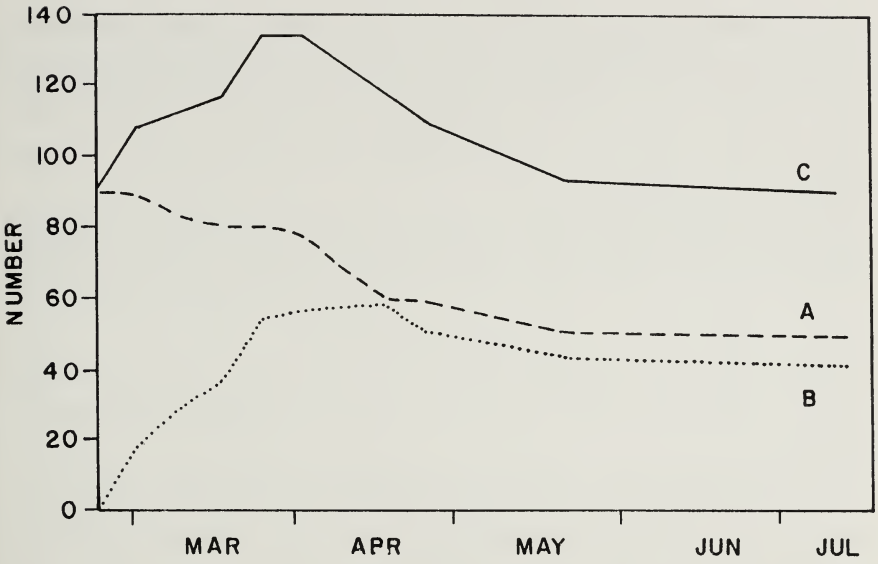


FIG. 4. Chick mortality and new nests of Magnificent Frigatebird. (A) Chick mortality, (B) "new" nestings, and (C) nests recorded = A + B.

It should be pointed out that the maximum number of chicks (from week 16 onward) was coincident with the highest captures of "sardine" by the commercial fishermen.

Putting together the data at hand, some personal observations on the behavior of females and fledglings in the colony, and some references from the literature, we tried to explain the occurrence of distinct hatching peaks with the implication of differential laying. Considering seven weeks of incubation (Diamond 1973, pers. obs.), plus 22 weeks of chicks' nest permanence (see growth), plus 26 weeks of females' post-fledging attendance (Trivelpiece and Ferraris 1987), we get a total of 55 weeks of females' care. Females with chicks hatched at weeks 7, 12, 17, and 23 (Fig. 2) could be in position of courtship at weeks 10, 15, 20, and 26 of the following year, respectively. In this way, the hypothesis of Diamond (1973) postulating biennial breeding for females is reduced to a little bit more than a year, increasing considerably the reproductive capacity of the colony.

←

FIG. 3. Average data and calculated curve of the pooled sample (1985 and 1986) for: (A) mass and (B) curves calculated for each measurement, as percentages of their respective asymptotes.

Reville (1988) suggested that most of the nests that failed during the first half of the laying season will contain a new displaying male or courting pair soon afterwards. In our case, it has to be considered that 46% of eggs or chicks died at some stage of development, therefore, their parent females would have been available for entering the first or second laying periods of the next year.

The calculated curves presented here lie between the two sets of data of supposed males and females obtained by Diamond (1975) at Aldabra, although the curves proposed by Diamond did not have a statistical basis. In the present study, as well as in the one by Trivelpiece and Ferraris (1987), information was insufficient to determine sex and thus calculate separate curves. The highest deviations from the mean were at 100 days, which, as Diamond stated, is the age when sexual dimorphism becomes apparent.

At hatching the chick is altricial, requiring full time parental attendance. From the mass growth curve, using the results (*cif.* fig. 1) presented by Dunn (1976), we assume endothermy (in the sense used by that author) is acquired at about 3–4 weeks, which agrees with the reports of Diamond (1972). A prolonged phase of non-accelerated growth is apparent and is more conspicuous for mass, wing, and wingspan. This phase is much smaller and less evident for the culmen. In spite of the differences shown in the slow growing phases, the general growth pattern is harmonic in the sense that, at the end of the main growth period, all structures have acquired their adult characteristics at about the same time (except mass, which actually decreases after a maximum value).

At hatching, the culmen is proportionately larger than other structures. This might be related to a fast development necessary for the acquisition of thermoregulation (Dunn 1975) as well as defense and acquisition of energy reserves. It is supported by the observation that the parents gradually spend less time at the nest directly caring for the chicks, coming back mainly to feed them.

Although Reville (1988) suggested that the main cause of nesting failure in the Great Frigatebird is due to usurpation of nests by unpaired males, in our study the main cause of nesting failure was due to robbery of materials from nests with eggs or chicks not older than three weeks and not to usurpation of nests by males. For older chicks, the main factor causing mortality was wind. On several occasions, after periods of gusty winds, broken branches were found on which there were one or several nests or fallen chicks. Fallen chicks soon die, since they are incapable of moving around once they fall from the nest. Generally, they become entangled or break their wings. There was no observed predation during the study. It is interesting that the number of active nests at the end of six

months was also 90 which undoubtedly indicates a high degree of replacement of nesting pairs. This agrees very well both with the suggestion of Reville (1988) and the hypothesis of reproductive waves or batches.

ACKNOWLEDGMENTS

We thank the fishermen of the "Las Tijeras" fishing camp at Isla Santa Margarita, especially Braulio Zumaya, for their understanding and support given during our field work. The field and data processing work of Leopoldo Moreno is gratefully acknowledged. We thank Daniel Anderson, Charles Collins, Ellis Glazier, Peter Whitehead, and Neil P. Bernstein for careful reading and reviewing of the manuscript.

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Wilson Bull., 107(2), 1995, pp. 338–358

INTENSITY AND CHRONOLOGY OF POSTREPRODUCTIVE MOLTS IN MALE CANVASBACKS

JONATHAN E. THOMPSON[1] AND RONALD D. DROBNEY[2]

ABSTRACT.—We studied molt intensity and chronology in male Canvasbacks (*Aythya valisineria*) from termination of reproductive activities until fall migration (May–October) in 1989–1990. During this period, male Canvasbacks underwent prebasic, down, and partial prealternate molts. Males arrived on molting habitat already undergoing light prebasic molt. Total molt intensity increased to moderate levels in late preflightless birds and remained at this intensity through the postflightless period. Contour plumage molt intensity was reduced in staging birds concurrent with declining ambient temperatures and fall migration. Prebasic body molt was most intense in late preflightless birds, while peak prealternate molt occurred during the postflightless period. Remigial molt occurred from late July through August near completion of prebasic body molt. Prealternate molt began concurrent with late remigial molt and was not completed in male Canvasbacks before fall migration from central Alberta. Synchrony in the timing of remigial and prealternate molts suggests that these molts were probably under photoperiodic regulation in male Canvasbacks. Down replacement occurred throughout the postreproductive period but reached peak intensity in late preflightless, flightless, and postflightless birds. Only light down molt still occurred in staging Canvasbacks. All male Canvasbacks examined underwent the normal progression of postreproductive molts regardless of age; however, yearling males initiated prebasic molt earlier than birds ≥2 years old. Male Canvasbacks extended postreproductive molts over a period of six months which minimized the daily nutritional requirements for plumage growth. *Received 21 Mar. 1994, accepted 10 Nov. 1994.*

Determining the intensity and chronology of molts in waterfowl (Anseriformes) is necessary to understand nutritional demands throughout the annual cycle. Molt is a productive process involving nutrient demands in addition to those for basal metabolic requirements, reproduction, and activity (King 1974). Nutrient requirements during molt arise primarily from an increased need for protein to meet the amino acid demands of epidermal keratin synthesis. Elevated energetic demands during molt originate from energy deposited in plumage and physiological processes (i.e., elevated somatic protein metabolism, alterations in water balance, increased blood volume, cyclic osteoporosis) that birds undergo to facilitate keratin synthesis (King 1980). Nutrient and energy demands in addition to those for plumage may originate from requirements for synthesis of feather sheaths, integument, and other epidermal structures replaced during molt (Murphy and King 1986, King and Murphy 1990).

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Male Canvasbacks (*Aythya valisineria*) molt primarily on large athalassic and subsaline wetlands in the aspen parklands and southern boreal forest regions of central and western Canada (Bergman 1973, Bailey 1983). During the postreproductive period, extending from termination of breeding activities until departure for fall migration, adult male Canvasbacks undergo prebasic, down, and partial prealternate molts. Little is known about the influence of molt intensity and chronology on nutritional requirements and timing of other energy demanding events (e.g., fall migration) during this period. Furthermore, most studies on molt in ducks (Anatinae) investigate only patterns of contour feather replacement and neglect down plumage molt. Our study reports intensity and chronology of feather replacement during prebasic, prealternate, and down molts in postreproductive male Canvasbacks molting in central Alberta. This research was conducted as part of a broader study that focused primarily on the nutritional tactics of Canvasbacks during molt (Thompson 1992).

STUDY AREA AND METHODS

Beaverhill Lake (53°27′N, 112°32′W) in the aspen parkland biome (Bird 1930, Strong and Leggat 1981) of east-central Alberta is traditionally used by molting and fall migrant Canvasbacks (Lister 1979). This large lacustrine wetland (Cowardin et al. 1979) covers approximately 139 km^2 in a shallow glacial depression with an average water depth of <1 m throughout most of the basin. The northeastern sector of Beaverhill Lake is a large delta-like marsh with expansive bays and extensive emergent macrophyte growth. Hardstem bulrush (*Scirpus acutus*) dominates deepwater marsh zones, with small stands of great bulrush (*S. validus*) occurring on shallower alkaline mud flats. Nearshore zones with lower alkalinity are dominated by cattail (*Typha* spp.). Submergent macrophyte growth generally begins 50–75 m from the lakeshore and varies markedly in distribution throughout the wetland. Sago pondweed (*Potamogeton pectinatus*), an important Canvasback food (Bartonek and Hickey 1969, Bergman 1973, Austin et al. 1990, Thompson 1992), is the dominant submersed aquatic plant forming large monotypic stands throughout the basin. Extensive pondweed beds occur in northern and southwestern regions of the lake and receive heavy use by molting and migrant waterfowl.

Male Canvasbacks (N = 143) were collected by shooting along traditionally used flight corridors and foraging sites from late May through October in 1989 and 1990. Additionally, some flightless birds were collected from a boat on calm days when they could be observed diving. Coloration of basic and alternate generations of contour plumage in male Canvasbacks were distinct in all tracts that underwent both molts (See descriptions in Palmer 1976) permitting reliable discrimination of stage of molt. Specimens were categorized into plumage classes using the following terminology and molt characteristics: (1) Early Preflightless (N = 32), early to intermediate stages of prebasic molt (≤50% basic plumage in capital and side-flank regions); (2) Late Preflightless (N = 28), advanced prebasic molt (> 50% basic plumage in capital and side-flank regions); (3) Flightless (N = 27), definitive basic plumage and incoming primaries and secondaries <80% of final length; (4) Postflightless (N = 29), early to intermediate stages of prealternate molt (≤50% alternate plumage in the capital and side-flank regions) and primaries and secondaries with sufficient growth for flight (>80% of mature length); and (5) Staging (N = 27), advanced prealternate molt (>50% alternate

TABLE 1

GENERAL CHRONOLOGY AND DURATION OF MOLT STAGES FOR ADULT MALE CANVASBACKS IN CENTRAL ALBERTA

Molt stage	Year	
	1989	1990
Early preflightless	21 May–29 June	22 May–2 July
Late preflightless	20 June–12 August	27 June–28 July
Flightless	22 July–6 September	23 July–5 September
Postflightless	26 August–22 September	27 August–24 September
Staging	21 September–14 October	24 September–19 October

plumage in capital and side-flank regions). General chronology and duration of molt stages were based on time budget observations (Thompson 1992) (Table 1).

Molt terminology follows that of Humphrey and Parkes (1959) except that remigial molt, which is part of prebasic molt, is discussed independently because of its significant nutrient requirements (Thompson 1992). Molt of down plumage is discussed separately because current molt terminology was developed exclusively from, and for description of, contour feather replacement patterns (See Humphrey and Parkes 1959). Each specimen was examined for contour plumage and down molt in 20 feather tracts comprising nine major plumage regions (Table 2). Separate scores of molt intensity were recorded for down and contour plumage in each tract. Plumage region and feather tract terminology were adapted from Billard and Humphrey (1972) and Titman et al. (1990).

Molt was detected by observing empty feather follicles and partially or fully ensheathed feathers (i.e., pinfeathers or blood quills). Molting contour and alar feathers were identified by presence of a vascularized calamus (Miller 1986). Incoming down feathers were distinguished from growing contour feathers by their small size and lack of a distinct basal calamus (Lovvorn and Barzen 1988). Distinction of molting feathers was most difficult in the capital region because of small contour and down plumage.

TABLE 2

ANATID PLUMAGE REGIONS AND THEIR CORRESPONDING FEATHER TRACTS[a]

Plumage regions	Feather tracts
Capital	Crown, facial, chin-throat, neck
Anterior ventral and spinal	Upper chest, upper back, center chest
Side-flank	Side chest, flanks
Scapular	Scapulars
Ventral	Belly
Posterior spinal	Lower back, rump
Tail coverts	Upper tail coverts, lower tail coverts
Rectrix	Rectrices
Wing	Primaries, secondaries, tertials, wing coverts

[a] Adapted from Billard and Humphrey (1972) and Titman et al. (1990).

Scoring of molt was done externally to minimize damage to tissues used in subsequent carcass composition analyses (Thompson 1992). All tracts were examined for contour plumage and down molt using the technique described by Greenwood et al. (1983). Each tract was scored using the following designations based on estimation of percent occurrence of pinfeathers: 0 = no molt, 1 = light molt (1–15% pinfeathers), 2 = intermediate molt (>15–40% pinfeathers), and 3 = heavy molt (> 40% pinfeathers). A mean regional, tract, or total molt score of 0 indicated absence of molt; 0.01–1.00 light molt; 1.01–2.00 intermediate molt; and 2.01–3.00 heavy molt. It should be noted that in the following discussion, peak seasonal molt intensity does not necessarily correspond with heavy molt intensity but instead represents the highest molt intensity observed in a given plumage region or feather tract during the postreproductive period.

Molt scores within plumage regions were calculated by summing scores of all feather tracts within a region and dividing by the number of regional subdivisions. Total molt scores were derived by averaging the nine regional molt scores. Nonparametric statistical procedures were used for data analysis because molt scores frequently exhibited bimodal or skewed distributions and heterogeneity of variances. Differences in molt intensity between plumage classes were determined using Kruskal-Wallis one-way analysis of variance tests (PROC NPAR1WAY; SAS Institute 1985). If significant variation ($P < 0.05$) occurred in the overall model, contrasting plumage classes were determined using Dunn's multiple comparisons test (Daniel 1990).

RESULTS AND DISCUSSION

Contour feather molt intensity.—Mean tract, regional, and total molt scores for each plumage class are presented in Table 3. Molt intensity data from 1989 and 1990 were pooled due to lack of variation ($P > 0.05$, Kruskal-Wallis ANOVA) between years in regional and total molt scores. Conversely, all plumage regions and feather tracts exhibited significant ($P < 0.05$) variation in mean molt intensity between plumage classes except for the facial tract ($H = 6.99$, $P = 0.14$). Age-related differences in molt intensity among adult male Canvasbacks (≥2 years old) were not apparent, since birds in this age class were undergoing definitive molt cycles (Palmer 1976). Only seven yearling males were collected when molting from Alternate I into definitive basic plumage. These specimens were consistently in advanced prebasic molt relative to older birds suggesting earlier initiation of this complete molt in yearling males.

Total molt score: Molt intensity increased from the early preflightless to the late preflightless period as prebasic body molt advanced (Table 3). Molt intensity remained elevated during the flightless and postflightless periods while birds were undergoing overlapping periods of prebasic and prealternate molts. Molt intensity declined from the postflightless to the staging period as prealternate molt was completed or reduced in many feather tracts (Table 3).

Early preflightless: Canvasbacks in this molt stage exhibited molt in all plumage regions indicating rapid progression of prebasic body molt as reproductive activities subsided. Prebasic molt in the capital, side-flank,

Table 3

Mean Molt Scores in the Plumage Regions and Feather Tracts of Postreproductive Male Canvasbacks Molting in Central Alberta

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[c]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Capital	12.11	0.02	1.66 (0.06)[f]	NS	1.60 (0.06)	NS	1.43 (0.07)	**	1.71 (0.06)	*	1.45 (0.08)
Crown	12.62	0.01	1.90 (0.07)	NS	1.70 (0.09)	NS	1.46 (0.10)	NS	1.69 (0.09)	NS	1.55 (0.09)
Facial	6.99	0.14	1.50 (0.09)	NS	1.53 (0.09)	NS	1.39 (0.09)	NS	1.63 (0.09)	NS	1.28 (0.11)
Chin–throat	17.36	0.0016	1.63 (0.09)	NS	1.40 (0.09)	NS	1.64 (0.09)	NS	1.91 (0.05)	*	1.62 (0.09)
Neck	23.37	0.0001	1.60 (0.09)	NS	1.77 (0.08)	***	1.21 (0.08)	**	1.63 (0.09)	NS	1.34 (0.09)
Side-flank	69.41	0.0001	2.00 (0.07)	***	2.52 (0.06)	***	1.50 (0.08)	***	2.55 (0.06)	NS	2.34 (0.08)
Side chest	72.63	0.0001	1.29 (0.11)	***	2.26 (0.11)	***	1.52 (0.10)	***	2.78 (0.07)	***	2.00 (0.12)
Flanks	63.94	0.0001	2.71 (0.08)	NS	2.77 (0.08)	***	1.48 (0.11)	***	2.31 (0.08)	*	2.69 (0.09)
Anterior ventral and spinal	59.27	0.0001	1.16 (0.11)	***	2.11 (0.08)	***	1.41 (0.08)	***	1.98 (0.04)	NS	1.79 (0.07)
Upper back	31.50	0.0001	1.31 (0.13)	**	1.94 (0.11)	***	1.21 (0.08)	NS	1.17 (0.07)	*	1.55 (0.09)
Upper chest	22.17	0.0002	1.31 (0.18)	**	2.13 (0.17)	**	1.33 (0.13)	*	1.85 (0.10)	NS	2.00 (0.10)
Center chest	77.63	0.0001	0.97 (0.11)	***	2.29 (0.11)	**	1.65 (0.12)	***	2.83 (0.07)	***	1.93 (0.13)

TABLE 3
CONTINUED

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H^b	$P > H^c$	EP (32)[d]	P^e	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Ventral (belly)	82.69	0.0001	1.23[f] (0.08)	***	1.97 (0.07)	**	1.39 (0.09)	***	2.72 (0.08)	***	1.68 (0.10)
Scapular	65.63	0.0001	2.52 (0.09)	NS	2.74 (0.08)	***	1.67 (0.09)	NS	1.94 (0.06)	NS	2.18 (0.07)
Posterior spinal	72.78	0.0001	0.84 (0.08)	***	1.55 (0.09)	NS	1.82 (0.09)	NS	2.05 (0.07)	*	1.76 (0.07)
Lower back	67.98	0.0001	0.76 (0.09)	***	1.53 (0.09)	*	2.07 (0.13)	NS	1.94 (0.08)	**	1.41 (0.10)
Rump	68.99	0.0001	0.91 (0.09)	***	1.57 (0.10)	NS	1.55 (0.09)	**	2.16 (0.11)	NS	2.11 (0.06)
Rectrix (rectrices)	80.19	0.0001	0.39 (0.09)	***	1.23 (0.18)	***	2.68 (0.10)	***	1.16 (0.10)	NS	0.98 (0.13)
Tail covert	48.01	0.0001	1.65 (0.12)	*	2.12 (0.12)	***	1.52 (0.08)	***	2.52 (0.07)	**	2.04 (0.09)
Upper tail coverts	40.44	0.0001	1.51 (0.12)	*	2.00 (0.13)	***	1.29 (0.09)	***	2.26 (0.09)	**	1.63 (0.11)
Lower tail coverts	36.53	0.0001	1.79 (0.18)	NS	2.23 (0.13)	*	1.75 (0.11)	***	2.77 (0.08)	NS	2.44 (0.11)
Wing	93.76	0.0001	0.01 (0.01)	*	0.14 (0.03)	***	2.66 (0.05)	***	0.25 (0.05)	NS	0.11 (0.03)
Primaries	112.10	0.0001	0.00 (0.00)	NS	0.00 (0.00)	***	3.00 (0.00)	***	0.50 (0.11)	NS	0.24 (0.08)

TABLE 3
CONTINUED

Feather regions and traets	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[e]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Secondaries	144.94	0.0001	0.00[f]	NS	0.00	***	3.00	***	0.00	NS	0.00
			(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Tertials	103.13	0.0001	0.03	NS	0.38	***	2.86	***	0.20	NS	0.14
			(0.03)		(0.10)		(0.07)		(0.07)		(0.07)
Wing coverts	97.81	0.0001	0.03	NS	0.14	***	1.75	***	0.30	NS	0.07
			(0.03)		(0.07)		(0.16)		(0.09)		(0.05)
Total molt score	62.90	0.0001	1.21	***	1.78	NS	1.80	NS	1.87	**	1.68
			(0.06)		(0.04)		(0.05)		(0.02)		(0.05)

[a] Molt periods include early preflightless (EP), late preflightless (LP), flightless (FL), postflightless (PF), and staging (ST).
[b] Kruskal-Wallis test statistic.
[c] Overall probability from Kruskal-Wallis test that molt scores differ by stage of molt.
[d] Sample size.
[e] Probability from Dunn's multiple comparisons test that adjacent means differ by chance; * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, NS = $P > 0.05$.
[f] Standard error of mean.

scapular, and tail covert regions of male Canvasbacks was initiated late in the breeding season as nearly all birds arriving on molting habitat exhibited some degree of molt in these regions. Lovvorn and Barzen (1988) recorded low intensity prebasic molt in capital and body tracts of breeding male Canvasbacks in Manitoba, but the exact locations of molt within these regions were not reported. Capital and scapular regions reached peak prebasic molt intensity in early preflightless Canvasbacks, whereas wing, rectrix, and posterior spinal regions showed only light, sporadic molt.

Late preflightless: Intensity of prebasic molt increased from the early preflightless period in the side-flank, anterior ventral and spinal, ventral, posterior spinal, rectrix, tail covert, and wing regions of late preflightless Canvasbacks (Table 3). Feather replacement intensity was typically similar within plumage regions, but most molting feathers in the side-flank region occurred in the side chest tract. Capital tracts molted at moderate intensity, and scapulars continued to molt heavily as observed in early preflightless birds. Anterior ventral and spinal, ventral, and tail covert regions reached the maximum prebasic molt intensity. The capital, ventral, posterior spinal, and rectrix regions had moderate molt intensity, while the side-flank, anterior ventral and spinal, scapular, and tail covert regions molted heavily. Only the wing region maintained light prebasic molt intensity in late preflightless Canvasbacks.

Flightless: Canvasbacks in this period reduced molt intensity from the late preflightless period in the side-flank, ventral, anterior ventral and spinal, scapular, and tail covert regions as prebasic body molt was completed (Table 3). Capital molt intensity remained unchanged from late preflightless levels but decreased ($P < 0.05$) in comparison to early preflightless molt intensity. During intermediate to late remigial growth, prealternate molt was initiated in the capital region and flanks. Overall, the posterior spinal region maintained similar molt intensity to late preflightless levels; however, one regional subdivision, the lower back tract, increased prebasic molt intensity (Table 3). Capital, ventral, and posterior spinal regions continued to molt at moderate levels similar to late preflightless birds, while the side-flank, anterior ventral and spinal, scapular, and tail covert regions decreased from heavy molt intensity during the late preflightless period to moderate levels in flightless birds (Table 3). Wing and rectrix regions reached peak prebasic molt intensity in flightless birds as all feather tracts in these plumage regions molted heavily.

Postflightless: Following remigial molt, Canvasbacks initiated extensive prealternate molt in the capital, side-flank, anterior ventral and spinal, ventral, and tail covert regions. Intensity of prealternate molt was greatest in the neck, flanks, side chest, upper chest, center chest, and upper and

lower tail covert feather tracts. Detection of both prebasic and prealternate molt in the tail covert region was possible because these tracts were designated as a separate region from the rectrices which are replaced only once per plumage cycle during prebasic molt in pochards (i.e., members of the genus *Aythya*) (Palmer 1976). Some molt studies have erroneously included the rectrices and tail coverts in a single plumage region (see Austin and Fredrickson 1986) thereby grouping tracts with inherently different molt patterns. Overlap in completion of prebasic molt and initiation of prealternate molt in the scapular region masked detection of increased molt intensity in this region. The posterior spinal region showed no change in overall molt intensity from the flightless period; however, the rump tract showed increased prebasic molt intensity (Table 3). Rectrix and wing molt declined markedly from the flightless to the postflightless period as prebasic molt neared completion in these regions (Table 3).

Staging: Prealternate molt intensity declined from the postflightless period in the capital, ventral, and tail covert regions of staging Canvasbacks (Table 3). Within these regions, prealternate molt intensity declined significantly from postflightless levels in the chin-throat, belly, and upper tail coverts (Table 3). Molt intensity remained unchanged from postflightless levels in the side-flank, anterior ventral and spinal, scapular, rectrix, and wing regions. Tracts within the anterior ventral and spinal region did not molt consistently during the staging period; the upper back tract increased prealternate molt intensity, while feather replacement declined in the center chest tract (Table 3). Acquisition of alternate scapulars in male Canvasbacks occurs gradually despite high molt intensity in staging birds and is not completed until later in fall migration or early winter (Lovvorn and Barzen 1988). Wing molt persisted only at negligible levels as primaries and tertials completed maturation.

Down molt intensity.—Mean down molt scores for plumage regions and tracts are presented in Table 4. Down plumage was replaced only once in male Canvasbacks during the postreproductive period. Only negligible down molt occurs outside the postbreeding period (Lovvorn and Barzen 1988), indicating that down is replaced only once annually in male Canvasbacks. Male Redheads (*Aythya americana*) also replace down plumage once per year concurrent with late prebasic and early prealternate molt (Bailey 1982).

Total down molt score: Replacement of down plumage increased from light intensity in the early preflightless period to moderate intensity in the late preflightless period (Table 4). Male Canvasbacks maintained moderate levels of down replacement from the late preflightless period through the postflightless period. Molt intensity declined to low levels in staging birds as down molt neared completion before fall migration (Table 4).

TABLE 4

MEAN DOWN MOLT SCORES IN THE PLUMAGE REGIONS AND FEATHER TRACTS OF POSTREPRODUCTIVE MALE CANVASBACKS MOLTING IN CENTRAL ALBERTA

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[e]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Capital	39.90	0.0001	0.70	*	1.13	NS	1.67	NS	1.39	***	0.40
			(0.13)[f]		(0.07)		(0.16)		(0.06)		(0.07)
Crown	30.10	0.0001	0.80	NS	1.23	NS	1.80	NS	1.64	***	0.50
			(0.14)		(0.12)		(0.20)		(0.13)		(0.15)
Facial	43.15	0.0001	0.47	*	1.00	NS	1.40	NS	1.14	***	0.00
			(0.13)		(0.11)		(0.13)		(0.10)		(0.00)
Chin–throat	27.48	0.0001	0.87	NS	1.15	NS	1.60	NS	1.29	***	0.25
			(0.19)		(0.10)		(0.16)		(0.13)		(0.13)
Neck	24.55	0.0001	0.67	NS	1.15	NS	1.87	NS	1.50	*	0.83
			(0.13)		(0.15)		(0.24)		(0.14)		(0.11)
Side-flank	36.41	0.0001	0.97	**	1.67	NS	1.79	*	1.25	**	0.62
			(0.14)		(0.09)		(0.13)		(0.10)		(0.10)
Side chest	30.40	0.0001	1.35	**	2.33	NS	2.50	*	1.71	NS	1.08
			(0.21)		(0.14)		(0.17)		(0.13)		(0.18)
Flanks	25.02	0.0001	0.59	NS	1.00	NS	1.07	NS	0.79	**	0.15
			(0.12)		(0.12)		(0.13)		(0.11)		(0.10)
Anterior ventral and spinal	41.82	0.0001	1.00	***	2.02	NS	1.76	**	1.25	NS	0.67
			(0.15)		(0.13)		(0.09)		(0.04)		(0.13)
Upper back	25.40	0.0001	0.93	*	1.57	NS	1.50	NS	1.08	*	0.47
			(0.15)		(0.17)		(0.14)		(0.08)		(0.17)
Upper chest	37.21	0.0001	1.00	***	2.21	*	1.43	*	1.00	NS	0.47
			(0.17)		(0.19)		(0.17)		(0.00)		(0.13)
Center chest	24.25	0.0001	1.07	***	2.29	NS	2.36	NS	1.69	NS	1.27
			(0.27)		(0.16)		(0.20)		(0.13)		(0.18)

TABLE 4
CONTINUED

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H^b	$P > H^c$	EP (32)[d]	P^e	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Ventral (belly)	36.92	0.0001	1.36 (0.13)[f]	***	2.54 (0.14)	NS	2.43 (0.14)	**	1.53 (0.13)	NS	1.07 (0.21)
Scapular	34.87	0.0001	0.71 (0.11)	NS	0.62 (0.14)	*	1.23 (0.12)	NS	1.40 (0.13)	***	0.15 (0.10)
Posterior spinal	39.38	0.0001	1.17 (0.06)	NS	1.46 (0.16)	***	2.36 (0.12)	NS	2.13 (0.09)	***	1.25 (0.14)
Lower back	27.45	0.0001	1.27 (0.12)	NS	1.57 (0.20)	**	2.43 (0.17)	NS	1.87 (0.09)	*	1.14 (0.18)
Rump	40.66	0.0001	1.07 (0.07)	NS	1.36 (0.17)	**	2.29 (0.13)	NS	2.40 (0.16)	***	1.36 (0.13)
Rectrix (rectrices)	41.39	0.0001	0.13 (0.09)	**	0.86 (0.14)	NS	1.27 (0.18)	NS	1.47 (0.13)	***	0.29 (0.13)
Tail covert	24.36	0.0001	1.03 (0.12)	***	1.96 (0.19)	NS	1.57 (0.13)	NS	1.20 (0.08)	NS	1.04 (0.13)
Upper tail coverts	21.09	0.0003	1.00 (0.09)	**	1.86 (0.23)	NS	1.47 (0.13)	NS	1.07 (0.07)	NS	1.00 (0.10)
Lower tail coverts	17.38	0.0016	1.06 (0.19)	**	2.07 (0.20)	NS	1.67 (0.19)	NS	1.33 (0.16)	NS	1.07 (0.22)
Wing	58.28	0.0001	0.00 (0.00)	**	1.02 (0.12)	***	2.48 (0.09)	NS	1.94 (0.15)	***	0.50 (0.14)
Primaries	56.82	0.0001	0.00 (0.00)	**	1.08 (0.18)	**	2.87 (0.09)	*	1.62 (0.18)	**	0.25 (0.18)

TABLE 4
CONTINUED

Feather regions and tracts	Molt status effects		Molt periods[a]								
	H[b]	$P > H$[c]	EP (32)[d]	P[e]	LP (28)	P	FL (27)	P	PF (29)	P	ST (27)
Secondaries	56.74	0.0001	0.00[f]	**	1.08	**	2.67	NS	1.92	***	0.17
			(0.00)		(0.18)		(0.13)		(0.21)		(0.11)
Tertials	52.54	0.0001	0.00	**	1.08	**	2.47	NS	2.23	**	0.75
			(0.00)		(0.14)		(0.13)		(0.17)		(0.25)
Wing coverts	42.66	0.0001	0.00	*	0.85	**	1.93	NS	2.00	**	0.83
			(0.00)		(0.19)		(0.18)		(0.23)		(0.27)
Total down molt score	49.78	0.0001	0.81	**	1.50	NS	1.84	NS	1.49	***	0.65
			(0.07)		(0.04)		(0.08)		(0.06)		(0.08)

[a] Molt periods include early preflightless (EP), late preflightless (LP), flightless (FL), postflightless (PF), and staging (ST).
[b] Kruskal-Wallis test statistic.
[c] Overall probability from Kruskal-Wallis test that molt scores differ by stage of molt.
[d] Sample size.
[e] Probability from Dunn's multiple comparisons test that adjacent means differ by chance; * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, NS = $P > 0.05$.
[f] Standard error of mean.

Lovvorn and Barzen (1988) indicated that down molt is complete in adult male Canvasbacks late in fall migration.

Early preflightless: Down molt began in all plumage regions except for the wings of early preflightless Canvasbacks. Molt was light in most regions except for the ventral, posterior spinal, and tail covert regions which had moderate molt intensity. Despite low overall levels of down replacement in the side-flank region, the side chest tract had moderate molt intensity, and reflected a pattern of down molt similar to the ventral region. Because down molt does not necessarily coincide with contour feather molt in designated feather tracts, it is probable that a better grouping of down plumage regions not based on contour feather location could be devised.

Late preflightless: Down molt increased from the early preflightless period in capital, side-flank, anterior ventral and spinal, ventral, rectrix, tail covert, and wing regions of late preflightless Canvasbacks (Table 4). Increased molt intensity represented peak seasonal down replacement in all regions except for the scapular, posterior spinal, and wing tracts. Average down molt scores were typically higher in flightless birds than late preflightless birds, but variation in molt intensity between plumage classes masked detection of significant differences. Only molt in scapular and posterior spinal regions remained unchanged from early preflightless levels. Molt intensity in most plumage regions proceeded at moderate levels except for the anterior ventral and spinal and ventral regions that were undergoing heavy down replacement. Only the scapular and rectrix regions still maintained light down molt intensity.

Flightless: Down molt continued at levels similar to late preflightless birds in the capital, side-flank, anterior ventral and spinal, ventral, rectrix, and tail covert regions of flightless Canvasbacks. Down molt increased to peak seasonal levels in the scapular, posterior spinal, and wing regions during remigial molt (Table 4). All plumage regions of flightless birds had moderate down molt intensity, with exception of the ventral, posterior spinal, and wing regions which were undergoing heavy levels of down replacement.

Postflightless: Intensity of down molt remained unchanged from flightless levels in the capital, scapular, posterior spinal, rectrix, tail covert, and wing regions of postflightless Canvasbacks. Patterns of molt within tracts of the wing region were not consistent because intensity of down replacement near the primaries decreased from flightless levels. The extent of down molt also declined from flightless birds in the side-flank, anterior ventral and spinal, and ventral regions (Table 4). Reduced molt intensity in the side-flank and anterior ventral and spinal regions was due primarily

to diminished down replacement in the side chest and upper chest tracts, respectively.

Staging: Canvasbacks in this plumage class had reduced down molt intensity in capital, side-flank, scapular, posterior spinal, rectrix, and wing regions in comparison to postflightless birds (Table 4). Down molt was similar within regions except for the side chest tract which maintained consistent down molt intensity despite an overall decrease in molt within the side-flank region from the postflightless period (Table 4). Molt of down plumage continued at similar levels in postflightless and staging birds in the anterior ventral and spinal, ventral, and tail covert regions. Replacement of down decreased in the upper back tract despite the lack of regional change in molt intensity in anterior ventral and spinal plumage (Table 4). Light down molt continued throughout the staging period in the capital, side-flank, anterior ventral and spinal, scapular, rectrix, and wing regions, while moderate molt intensity was maintained in the ventral, posterior spinal, and tail covert tracts. Staging male Canvasbacks had not completed down molt before fall migration from central Alberta.

Chronology and pattern of prebasic molt.—Prebasic molt in male Canvasbacks extended from mid-May through September and was a complete molt because head, body, rectrix, and remigial plumage was replaced. Male Canvasbacks initiate prebasic molt late in the breeding season (Lovvorn and Barzen 1988). Feather replacement begins in capital tracts, followed by scapulars, flanks, and tail coverts. Only the posterior spinal tracts continued prebasic molt into October in postflightless and staging Canvasbacks. The timing of prebasic molt in the posterior spinal region of male pochards is misleading, causing some researchers to consider it as prealternate molt (see Bailey 1982). Because feather follicles in the posterior spinal region are activated only once during the annual molt cycle, feathers of the lower back and rump tracts should be considered basic plumage (Humphrey and Parkes 1959, Palmer 1972) in male pochards.

Chronology of prebasic body molt varies with age in male Canvasbacks. Yearling males which had probably neither been paired nor participated in breeding activities arrived on molting areas first, often in advanced prebasic molt. Older males, which presumably had a more extended breeding effort, arrived on molting sites later, with only light prebasic molt in capital and side-flank regions. Breeding male Redheads began prebasic molt earlier in a year with abbreviated or no reproductive effort (Bailey 1982). During years with extended breeding seasons, prebasic body molt was temporally compressed in male Redheads before remigial molt.

Hochbaum (1944) suggested that variation in onset of prebasic molt in

male Canvasbacks was related to the bird's prior breeding status. He observed among captive birds that feather replacement began first in the earliest breeding males, followed by males paired to the latest nesting females, and finally nonbreeding males (typically yearlings), a sequence different from that which we observed in wild birds. Initiation sequence of prebasic molt among male ducks in several other species (Oring 1968, Palmer 1972, Bailey 1982) supports the pattern of molt progression we observed in wild Canvasbacks in that feather replacement was initiated first in yearling males which had probably not bred, followed by older, previously paired males. Hochbaum (1944) also suggested from his captive studies that male Canvasbacks >3 years old underwent only partial prebasic molt, with some birds molting directly from alternate to alternate head-body plumage. Most of the birds examined during our study were adult males, including many drakes that were at least three years old as determined by wing plumage characteristics (Serie et al. 1982). All specimens from this older age cohort underwent a normal progression of postreproductive molts and did not skip or undergo reduced prebasic molt as suggested by Hochbaum (1944). Studies of molt using captive Canvasbacks may have limited generalization to wild birds. Palmer (1972) warned that captivity can alter timing and duration of molt in waterfowl and that observations from captive birds should be considered speculative.

Most prebasic body molt was completed before male Canvasbacks shed their remiges or during early remigial growth. The posterior spinal region tracts, including the lower back and rump, were notable exceptions, with prebasic molt continuing through fall staging in October. Many feather tracts, particularly those in the capital and side-flank regions, initiated prealternate molt almost immediately upon completion of prebasic molt.

Chronology and pattern of prealternate molt.—Prealternate molt in male Canvasbacks began before completion of remigial molt and was an incomplete molt because the basic wing, rectrices, and plumage of the posterior spinal region were retained. Male Canvasbacks initiated prealternate molt when primaries were approximately 40% mature. There was a high degree of synchrony in onset of prealternate molt, suggesting photoperiodic regulation of this body molt in adult male Canvasbacks (see postflightless birds in Table 1). Feather replacement was first apparent in capital and side-flank regions in late August while birds were still flightless, but peak prealternate molt occurred in most plumage regions during the postflightless period in September when remigial growth was near completion. Scapulars were the last feathers to undergo prealternate molt, with peak replacement occurring during premigratory staging (Table 3). Low intensity molt in the scapulars of male Canvasbacks continues

throughout winter, increasing again in February, particularly in juveniles (Lovvorn and Barzen 1988).

Hochbaum (1944) suggested that some male Canvasbacks attained definitive alternate plumage by September. Hochbaum's conclusion may have been based on observation of birds at a distance that appeared to be in full alternate plumage in late September, but if examined more closely would likely have been undergoing various stages of prealternate molt. In fact, none of the birds we examined had completed prealternate molt even by late October. Prealternate molt is apparently not complete in adult male Canvasbacks until late fall migration in November (Lovvorn and Barzen 1988) which is earlier than in male Greater Scaup (*Aythya marila*) that do not attain definitive alternate plumage until late December (Billard and Humphrey 1972). In both species, adult males complete prealternate molt before juveniles (Billard and Humphrey 1972, Lovvorn and Barzen 1988).

Chronology and pattern of remigial molt and rectrix replacement.— Wing molt in male Canvasbacks began in the tertial tract as reported for male Gadwalls (Oring 1968). Some tertial molt occurred in early and late preflightless Canvasbacks, but most tertials did not molt until the flightless stage. The innermost tertials were replaced during both prebasic and prealternate molts in Canvasbacks as reported by Palmer (1976). Replacement of basic tertials began late in the postreproductive period and was completed by January (Lovvorn and Barzen 1988).

The earliest molting male Canvasbacks initiated wing molt in late July during both years of this study (Table 1). However, the peak number of flightless birds occurred consistently during the second week of August when 90% of males were undergoing remigial molt. Synchrony in timing of remigial molt in successive years indicated strong photoperiodic control of this molt in male Canvasbacks. Some male Canvasbacks were still flightless as late as the first week of September, but most males (88%) had regained flight by this time. Hochbaum (1944) reported that male Canvasbacks underwent remigial molt on Lake Manitoba from late July to late August, during the same period as birds in this study.

Primaries and secondaries of male Canvasbacks were lost in close synchrony. Several flightless drakes collected early in remigial molt still possessed several intact flight feathers despite the absence of most others. All remiges still present were easily removed indicating that they were close to being shed. Proximal remiges, including the secondaries and inner primaries of Canvasbacks, matured more rapidly than distal primaries, permitting flight at earlier stages of remigial growth. Similar patterns of remigial maturation occur in other ducks (Weller 1957, Oring 1968, Bailey 1982, Young and Boag 1981, Austin and Fredrickson 1986).

Field observations in central Alberta indicated that male Canvasbacks were flightless for a period of three to four weeks. Canvasbacks in Manitoba had a similar flightless period of two and one-half to four weeks (Hochbaum 1944). Other male pochards, including Redheads (Bailey 1982) and Ring-necked Ducks (*Aythya collaris*) (Mendall 1958) also have a 3–4 week flightless period in the wild.

Wing coverts were the last alar tract to be replaced in male Canvasbacks. Most lesser and median coverts were not replaced until remigial growth was 40% complete. However, greater primary and secondary coverts were lost shortly after emergence of remiges, as observed in male Redheads (Bailey 1982). Replacement of ventral wing coverts, including the axillars, occurred primarily during latter remigial growth. Maturation of axillars was not complete in several postflightless and staging birds we examined, accounting for the light molt intensity in the wing covert tract during these periods (Table 3). Molt of the dorsal lesser and median wing coverts was quite variable, with some birds replacing feathers in these tracts simultaneously; however, most birds retained a heterogeneous mixture of growing and old coverts. Gradual replacement of wing coverts may provide some degree of protection to the wing and small fragile blood quills of maturing coverts.

Male Canvasbacks replace their rectrices once per plumage cycle, primarily during the flightless period. However, rectrix molt was observed throughout the postreproductive season, increasing in intensity from the early preflightless period to peak feather replacement during remigial molt and then steadily declining through fall staging (Table 3). Most rectrix replacement was complete in adult male Canvasbacks before fall migration from central Alberta.

Other anatids have similar irregular patterns of rectrix replacement during the postreproductive period. Wishart (1985) reported that the timing of rectrix replacement in male American Wigeons (*Anas americana*) was inconsistent, but central tail feathers were typically replaced first. Male Mallards (*Anas platyrhynchos*) initiated rectrix molt before remigial molt and continued tail feather replacement until fall migration (Young and Boag 1981). Tail molt in male Common Mergansers (*Mergus merganser*) (Erskine 1971) and female Lesser Scaup (*Aythya affinis*) (Austin and Fredrickson 1986) has also been described as prolonged and irregular following the breeding season.

Chronology and pattern of down plumage molt.—Down molt began in early preflightless Canvasbacks but did not reach peak intensity until the late preflightless period (Table 4). Down plumage replacement occurs more gradually than contour feather molts in male Canvasbacks, similar to the pattern of down replacement in male Mallards (Young and Boag

1981). Most down is replaced during late prebasic and early prealternate contour feather molts (late July–early September) in flightless male Canvasbacks. Mallards (Young and Boag 1981) and Redheads (Bailey 1982) also replace most of their down plumage during the flightless period in late summer before onset of cooler water and ambient temperatures. Down molt declined in staging Canvasbacks, but was not complete before fall migration in late October. Lovvorn and Barzen (1988) reported low levels of down molt continuing through fall in male Canvasbacks but negligible down molt by early winter.

Energetic aspects of postreproductive molts.—The adaptiveness of the ephemeral basic head-body plumage in male Canvasbacks is less apparent than the alternate generation which serves a strong function in mate selection. Furthermore, it is difficult to argue that basic plumage of male Canvasbacks makes them more cryptic during the flightless period because birds occupy open water habitats during remigial molt, making them readily visible (Thompson 1992). It is much easier to envision the survival advantage of drab colored basic plumage in male dabbling ducks which typically undergo wing molt in heavily vegetated marsh habitats where camouflage reduces detection by potential predators. Bailey (1982) suggested that the time basic plumage was worn by male Redheads served as a buffer period to ensure higher quality alternate plumage during spring courtship and breeding activities. Therefore, basic plumage was viewed as a transitional generation that delayed acquisition of alternate plumage, thereby reducing wear on the plumage that serves an epigamic role later in the annual cycle.

The higher quality alternate head-body plumage (Wielicki 1986) provides insulation for birds during the colder periods of the annual cycle and functions in epigamic display (Weller 1967). Male Canvasbacks may acquire alternate plumage far in advance of pairing because of the energetic advantage of undergoing extensive body molt during a warmer period of the year. If prealternate molt was delayed until late winter, just before onset of spring courtship, increased thermoregulatory costs from heat loss through blood-filled pinfeathers might be too great an energetic burden to incur concurrently with other energy requirements for maintenance and spring migration. Furthermore, the more vivid and bolder alternate plumage of older male Canvasbacks may function to establish dominance in large wintering aggregations within which individuals compete for optimal feeding locations (Alexander and Hair 1977).

Male Canvasbacks minimized per diem nutrient demands for plumage growth by extending the duration of postreproductive molts over six months. Low daily nutritional requirements for epidermal keratin synthesis allowed overlap in the timing of prebasic body molt and molt migra-

tion in the early preflightless period, both prebasic and prealternate body molts and down molt with remigial molt in flightless birds, and prealternate molt with fall migration in staging Canvasbacks. Similarly, female Canvasbacks continued prebasic body and down molts concurrent with spring migration and rapid follicular growth (Lovvorn and Barzen 1988).

Heitmeyer (1987) suggested that molt in anatids was timed to minimize or prevent overlap with other energy demanding events (e.g., migration and reproduction) in the annual cycle. However, this hypothesis presumes that daily nutritional requirements for molt are too high to sustain feather growth during other periods of elevated energy demands. By extending the duration of molt, birds can reduce daily nutritional requirements for plumage synthesis to the extent that temporal separation of molt from other energy demanding events in the annual cycle may not be necessary. Plumage growth concurrent with reproduction and migration in male and female Canvasbacks indicates that temporal overlap of molt and other energy demanding processes can occur in anatids with extended molt periods and low per diem nutritional requirements for molt.

ACKNOWLEDGMENTS

Funding for this project was provided by the North American Wildlife Foundation through Delta Waterfowl and Wetlands Research Station, the E. K. Love Fellowship at the Univ. of Missouri (UM), and the Missouri Cooperative Fish and Wildlife Research Unit (UM, U.S. Fish and Wildlife Service, Missouri Dept. of Conservation, and the Wildlife Management Institute cooperating). Many aspects of this project benefitted from support and advice by B. D. J. Batt and M. G. Anderson. Furthermore, this research would not have been possible without the generous cooperation and logistic support provided by W. M. Barrett, J. Nolan, and L. Roy of the Alberta Environmental Centre; K. J. Lungle of Alberta Forestry, Lands and Wildlife; G. R. Stewart of Ducks Unlimited Canada; B. C. Turner of the Canadian Wildlife Service; and landowners adjacent to Beaverhill Lake. Dedicated field assistance for this project was provided by D. W. Blair, C. A. Deschamps, D. H. Kusnierz, M. J. Petrie, J. P. Schneider, and A. J. Wyss. We thank C. D. Ankney, L. H. Fredrickson, and R. D. Titman for reviewing earlier drafts of this manuscript.

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Wilson Bull., 107(2), 1995, pp. 359–365

SHORT COMMUNICATIONS

Molt chronology of male Mallards wintering in Missouri.—Patterns of molt vary among groups and species of waterfowl (Family Anatidae). Geese, swans, and whistling ducks have a single annual molt, generally initiated during summer; most other waterfowl have two body molts, one (the prealternate molt) initiated during summer or fall and the other (the prebasic molt) initiated at various times of the year, dependent upon species and sex specific strategies (Hohman et al. 1992). Additional molts (supplemental molts) have been reported for the Oldsquaw (*Clangula hyemalis*) (Salomonsen 1941) and may exist in other waterfowl species.

Molt chronology has been examined for a number of waterfowl species, and several factors have been shown to influence the timing of molt. Species specific differences exist even among closely related species (e.g., dabbling ducks of the tribe Anatini) and are directly related to pairing strategies; males of species that form pair bonds early in the fall or winter complete the prealternate molt earlier than those that pair later (Hohman et al. 1992). Sexual differences in molt chronology of dabbling ducks are related to role differences in the reproductive cycle. Females undergo a prolonged prebasic molt during spring and early summer to provide additional concealment during nesting, whereas males complete a short prebasic molt during mid-summer and retain their alternate plumage for a longer period (Palmer 1972). Most male dabbling ducks do not pair until the alternate plumage is in an advanced stage of development (Klint 1980; Wishart 1983; Paulus 1984; Hohman and Ankney, in press), and young males often complete the prealternate molt later than adults (Wishart 1983, Hohman et al. 1992).

Although summer molt chronology of male Mallards (*Anas platyrhynchos*) has been studied in Manitoba (Young and Boag 1981) and winter molt chronology of female Mallards has been studied in Missouri (Heitmeyer 1987), comparable information for wintering males is currently not available. This study quantifies molt of male Mallards throughout winter in southeastern Missouri and relates molt chronology to month, year, age, and pair status.

Study area and methods.—We conducted this study on Mingo National Wildlife Refuge and the adjacent Duck Creek Wildlife Management Area in southeastern Missouri. Collectively, these areas comprise the remnants of the once extensive Mingo Swamp (Korte and Fredrickson 1977), a mosaic of eight major habitat types including (1) lowland hardwood forests, (2) dead tree, (3) scrub/shrub swamp, (4) open water, (5) marshes, (6) moist-soil, (7) farmland, and (8) ditches and creeks; over 65% of the area is comprised of habitats dominated by woody vegetation (Heitmeyer 1985). Approximately 9300 ha of the Mingo Swamp flood during winters of average precipitation.

We collected male Mallards (N = 276) by shooting in the Mingo Swamp from October through March 1983–1984, 1984–1985, and 1985–1986. Pair status was determined by watching individuals for 5–30 min prior to collection and evaluating synchrony in movement between mates, isolation of pairs or single males, and stereotypic behaviors associated with pairs (e.g., copulation, mutual display, and female tolerance of males). Mallards were aged by plumage (Krapu et al. 1979), bursa, and penal characteristics.

Feathers were counted as Mallards were plucked during 1983–1984 and 1984–1985. In 1985–1986, blood quills were counted on everted skins. Titman et al. (1990) reported that molt scoring using grab samples of feathers from various regions and subregions is more reliable than using everted skins. We checked our scoring approach during 1985–1986 by sampling with grab samples on most everted skins that had visible blood quills and 30 skins with no visible blood quills. All ducks examined in this way were scored the same by both approaches.

TABLE 1

NUMBER OF INCOMING FEATHERS IN EACH OF 20 MALLARD FEATHER AREAS REQUIRED FOR ASSIGNMENT TO MOLT SCORE 0–2

Feather region[a]/area	Molt score		
	0	1	2
Capital			
Crown	<10	10–50	>50
Facial	<10	10–50	>50
Chin–throat	<10	10–50	>50
Neck	<10	10–50	>50
Scapulohumeral			
Scapulars	0	1–4	>4
Spinal			
Upper back	<5	5–10	>10
Lower back	<5	5–10	>10
Rump	<5	5–10	>10
Caudal			
Upper tail coverts	<5	5–10	>10
Tail	0	1–2	>2
Lower tail coverts	<5	5–10	>10
Ventral			
Belly	<5	5–10	>10
Chest-center	<5	5–10	>10
Chest-side	<5	5–10	>10
Side	<5	5–10	>10
Flank			
Flank	0	1–4	>4
Alar			
Primaries	0	1–2	>2
Secondaries	0	1–2	>2
Tertials	0	1–2	>2
Wing coverts	<5	5–10	>10

[a] Regions from Humphrey and Clark (1961).

Molt status was determined by methodology described by Austin and Fredrickson (1986), as modified from Billard and Humphrey (1972). Twenty feather areas were examined that corresponded to seven previously described feather regions (Humphrey and Clark 1961) (Table 1). Intensity scores (0–2) were assigned to each feather area based on the number of incoming contour feathers (Table 1). Molt-intensity scores for individual ducks were determined by summing the scores for the 20 feather areas (range = 0–40). Down molt and plumage aspect were not assessed in this study, but notes were recorded on plumage appearance of individuals that appeared unusual (e.g., the few that exhibited some basic feathers).

TABLE 2

GENERAL LINEAR MODEL USED TO DESCRIBE DIFFERENCES IN MOLT-INTENSITY OF MALE MALLARDS COLLECTED IN SOUTHEASTERN MISSOURI, WINTER 1983–1986

Source[a]	df	Sum of squares	*F*-value	$P > F$
Model[b]	47	3.08576337	2.55	0.0001
Error	228	5.87708902		
Corrected total	275	8.96285238		
Month	5	0.62005928	4.81	0.0003
Year	2	0.04172161	0.81	0.4464
Month × year	8	0.31241636	1.52	0.1529
Age	1	0.00477032	0.19	0.6675
Month × age	5	0.13549155	1.05	0.3884
Year × age	2	0.05933645	1.15	0.3182
Month × year × age	3	0.06455773	0.83	0.4760
Pair	1	0.00211130	0.08	0.7750
Month × pair	5	0.08087619	0.63	0.6789
Year × pair	2	0.01356378	0.26	0.7689
Month × year × pair	7	0.12670622	0.70	0.6702
Age × pair	1	0.00093448	0.04	0.8492
Month × age × pair	2	0.00352247	0.07	0.9340

[a] Year × age × pair and Month × year × age × pair were not tested because of insufficient degrees of freedom.
[b] Explained variance: $r^2 = 0.34$.

An analysis of variance model (Proc GLM) with type III sums of squares (SAS Institute Inc. 1991) was used to test if differences existed in mean molt-intensity scores among months, years, age, and pair status of individual ducks. A multiple analysis of variance model (MANOVA PROC GLM) with type III sums of squares (SAS Institute Inc. 1991) was used to test if differences existed in mean molt-intensity scores among these same variables in seven different feather regions. We only considered univariate analysis results from the MANOVA model if Wilk's Lambda tests were significant for individual variables or interaction terms. Duncan's new multiple range test was used to separate means that were determined to be significantly different. Non-normal percentage data were arcsine transformed before all analyses. A *G*-test (Sokal and Rohlf 1981) was used to determine if molt activity of male Mallards collected in March was independent of collection year. For this test, we categorized Mallards as those exhibiting no molt (molt-intensity score = 0), light molt (molt-intensity score = 1–9), or heavy molt (molt-intensity score >9). Significance was deemed appropriate in all tests at an alpha level of 0.05.

Results.—Mean molt-intensity scores of male Mallards varied seasonally (Table 2), with molt occurring most intensely in October and only negligibly between December and February (Fig. 1). Intermediate molt activity occurred in Mallards collected during November and March (Fig. 1). Despite the higher mean during March than during previous months, most male Mallards probably do not molt during spring, as indicated by the high percentage of nonmolting males (32%) and those with molt-intensity scores <10 (45%) collected in March.

Mean molt-intensity of male Mallards did not differ among years, age, or pair categories, nor were any interaction terms significant in the GLM ANOVA model (Table 2). Although year and month × year were not significant in the model, only 6.1% of Mallards collected

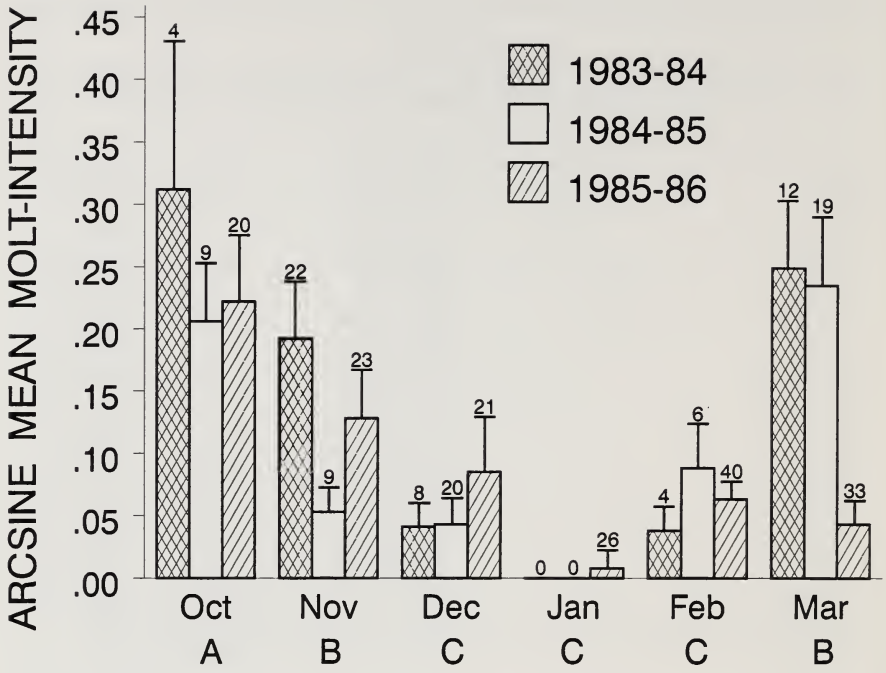

FIG. 1. Arcsine-transformed monthly molt-intensity scores (mean ± SE) of male Mallards collected in southeastern Missouri during three consecutive winters. Numbers above bars represent sample sizes. Months with the same letter below were not significantly different ($P > 0.05$) as determined by Duncan's new multiple range test.

during March 1986 had molt-intensity scores >9. A greater percentage of male Mallards were molting at this level during March of the previous two years (1984, 41.7% and 1985, 36.8%), and fewer were not molting at all (1984, 0%, 1985, 21.1%, and 1986, 54.5%, $G = 21.982$, df = 4, $P < 0.005$).

Month and year were the only variables or interaction terms that were significant in the MANOVA model comparing molt-intensity of various feather regions (month: Wilk's Lambda = 0.659, df = 35, $P = 0.0001$; and year: Wilk's Lambda = 0.879, df = 14, $P = 0.0105$). Monthly differences in molt activity were detected in the capital ($F = 2.86$, df = 5, $P = 0.0158$), scapulohumeral ($F = 8.85$, df = 5, $P = 0.0001$), spinal ($F = 4.35$, df = 5, $P = 0.0008$), and flank ($F = 5.50$, df = 5, $P = 0.0001$) regions; all of these regions exhibited similar patterns of declining molt activity during mid-winter, followed by an increase during early spring (Table 3). Although monthly differences were also detected in the caudal region ($F = 3.78$, df = 5, $P = 0.0026$), replacement of tail feathers was completed during November, and caudal molt was negligible after this time (Table 3). Monthly differences were not significant for the ventral and alar regions. Yearly differences were detected only in the caudal ($F = 3.50$, df = 2, $P = 0.0320$) and alar ($F = 4.10$, df = 2, $P = 0.0179$) regions, with greater molt activity occurring during 1983–1984 than during the following two winters.

Discussion.—Decline in molt-intensity of male Mallards from October through January

TABLE 3

ARCSINE MONTHLY MOLT-INTENSITY SCORES (MEAN ± SE) OF SEVEN FEATHER REGIONS OF MALE MALLARDS WINTERING IN SOUTHEASTERN MISSOURI

Feather region	Month					
	October (N = 33)	November (N = 54)	December (N = 49)	January (N = 26)	February (N = 50)	March (N = 64)
Capital	0.412 ±0.082	0.184 ±0.051	0.087 ±0.040	0.000 ±0.000	0.121 ±0.040	0.266 ±0.053
Scapulohumeral	1.111 ±0.118	0.776 ±0.101	0.150 ±0.051	0.060 ±0.033	0.188 ±0.068	0.376 ±0.073
Spinal	0.212 ±0.060	0.147 ±0.037	0.078 ±0.036	0.000 ±0.000	0.063 ±0.024	0.155 ±0.038
Caudal	0.230 ±0.068	0.125 ±0.032	0.050 ±0.034	0.000 ±0.000	0.025 ±0.015	0.032 ±0.011
Ventral	0.144 ±0.032	0.143 ±0.043	0.067 ±0.023	0.024 ±0.014	0.103 ±0.044	0.241 ±0.056
Flank	0.857 ±0.133	0.407 ±0.081	0.192 ±0.064	0.020 ±0.020	0.168 ±0.062	0.344 ±0.071
Alar	0.011 ±0.006	0.016 ±0.007	0.010 ±0.006	0.000 ±0.000	0.000 ±0.000	0.002 ±0.020

represented completion of the prealternate molt (Humphrey and Parkes 1959, Palmer 1976). All adult males and most juveniles in the Mingo Swamp completed or approached completion of the prealternate molt by early December. Most adults that were molting from October through December were in late molt stages, as indicated by a lack of basic plumage feathers and the general appearance of ducks that had completed the prealternate molt. Male ducks of many species can successfully pair during late stages of the molt, provided they appear in a complete alternate plumage (Wishart 1983, Paulus 1984). Most adult male Mallards wintering at the Mingo Swamp had probably completed enough of the prealternate molt prior to their arrival that they could successfully court and acquire mates, hence the reason for the lack of a relationship between pair status and molt activity in this study.

The increase in molt activity during March may represent a supplemental molt, as proposed for the Oldsquaw (Salomonsen 1941). Molt activity also increased in male Greater Scaup (*Arthya marila*) during March but was described as an interruption of the prealternate molt by Billard and Humphrey (1972). All male Mallards collected from December through March appeared to be in a full alternate plumage, suggesting that spring molt activity observed in this study was not a protraction of the prealternate molt but probably a supplemental molt. Spring molt activity has also been reported in other male dabbling ducks; e.g., Gadwalls (*Anas strepera*) (Paulus 1984) and American Wigeon (*A. americana*) (Wishart 1985), but spring molt has not been detected in Northern Pintails (*A. acuta*) (Miller 1986, Smith and Sheeley 1993). Molt-intensity of male Mallards was low on migration areas north of the Mingo Swamp (T. G. LaGrange, F. A. Reid, N. M. Gruenhagen, unpubl. data), indicating that spring molt activity probably is restricted to a portion of the population rather than being a molt initiated by all birds on wintering areas and completed during migration.

We suspect that the supplemental molt may serve to replace plumages worn during ad-

verse conditions, primarily because of yearly differences in percentages of males molting during March. Molt-intensity during March was less during 1986 (a mild winter) than during the previous two years, following harsh winters when Mallards were forced to migrate from the Mingo Swamp because of ice cover (Combs 1987). Spring molt activity also may be related to thermoregulatory needs or possibly be an evolutionary artifact that persists because of lack of strong selection pressure.

Acknowledgments.—This project was funded by U.S. Fish and Wildlife Service Contract #USDI-FWS-14-16-0009-83-945 (The School of Nat. Resour., Univ. of Missouri–Columbia cooperating) and Delta Waterfowl and Wetlands Research Center. The study is a contribution from the Gaylord Memorial Laboratory, Missouri Cooperative Wildlife Research Unit, and Missouri Agricultural Experiment Station, Project 183, Journal Series Number 11,772. Additional support was provided by the Edward K. Love Conservation Foundation and a Gregory Fellowship of the Univ. of Missouri–Columbia. Personnel of Duck Creek Wildlife Management Area and Mingo National Wildlife Refuge provided assistance. D. Jacques, D. F. McKenzie, M. Morris, D. Roster, and J. C. Ware assisted in collecting and dissecting ducks. We thank R. D. Drobney, E. K. Fritzell, J. J. Jones, M. K. Laubhan, and two anonymous reviewers for reviewing this manuscript.

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Wilson Bull., 107(2), 1995, pp. 365–371

Habitat use by wintering and breeding bird communities in relation to edge in an irrigated forest.—About 1% of the 2000 municipal sewage systems in the United States that apply wastewater to terrestrial habitats apply it to forested landscapes (W. E. Sopper, pers. commun.; Urie 1986). This is expected to increase as small, localized sewage systems are needed in nonagricultural areas (Nutter and Red 1986). Wastewater application changes structure and species composition of forest understory plants, distribution of fruit-producing plants, and abundance of invertebrates on the forest floor (Sopper and Kardos 1973, Lewis 1977, Mastrota et al. 1989, Rollfinke and Yahner 1990). Wastewater application also has been found to affect abundance and distribution of avian species, particularly those that forage and nest near ground level (e.g., Lewis and Sampson 1981, Rollfinke and Yahner 1990, Rollfinke et al. 1990). These avian studies, however, were relatively restricted in area or were based on mist-netting data collected only during the breeding season. Furthermore, establishment and maintenance of a wastewater-application system produces a considerable amount of edge habitat because of the network of irrigation pipes and access roads. In this study, my objective was to determine use of four habitat types by wintering and breeding bird communities in relation to distance from an edge from 1987–1991 in a forest-farmland landscape, part of which was affected by wastewater irrigation in central Pennsylvania.

Study area and methods.—I conducted the study on State Game Lands 176 in Centre County, Pennsylvania, from 1987–1991 (see details in Rollfinke and Yahner 1990, Rollfinke

et al. 1990). The irrigated sector of the study area contained a 200-ha wastewater-irrigation system that began operation in 1983. The system consisted of about 3100 rotating sprinklers along a network of lateral pipes, which pumped an average of 264 cm of wastewater annually during the study; this was about three-fold the normal annual precipitation (93 cm) in central Pennsylvania (Matula 1983). Wastewater sprayed from sprinklers reached a height of about 4 m and a radius of 10–15 m from each sprinkler nozzle; nozzles were spaced 26 m apart. The irrigated sector consisted of an intermix of approximately 50% forest and 50% farmland and was traversed by numerous unimproved access roads. The non-irrigated sector used in my study was forested and adjacent to the irrigated sector.

Maximum age of overstory trees (woody stems ≥1.5 m tall, >7.5 cm dbh) in both the irrigated and the non-irrigated sectors was about 65–70 years old. Principal overstory trees in both sectors were quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), scarlet oak (*Quercus coccinea*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), red maple (*Acer rubrum*), and pitch pine (*Pinus rigida*). Densities (no./ha) and basal areas (m^2/ha) of overstory trees were greater in the irrigated than in the non-irrigated sector (see details of vegetation in Rollfinke and Yahner 1990, Rollfinke et al. 1990), probably because wastewater irrigation promotes higher rates of tree growth (Sopper and Kardos 1973). Major understory trees (2.5–7.5 cm dbh) and shrubs (<2.5 cm in diameter) in both sectors were quaking aspen, red maple, rose (*Rosa* spp.), and Tartarian honeysuckle (*Lonicera tatarica*). Because of winter ice buildup from wastewater and subsequent stem breakage on understory trees and shrubs, understory trees and shrubs were about four-fold and three-fold less abundant on the irrigated than on the non-irrigated sector, respectively. Herbaceous ground cover was 57% on the irrigated sector compared with 5% on the non-irrigated sector. Ground cover on the irrigated sector was predominantly white snakeroot (*Eupatorium rugosum*), common pokeberry (*Phytolacca americana*), and Canada clearweed (*Pilea pumila*), which formed a lush layer of vegetation at least 2 m in height in some places. These differences in vegetation between the irrigated and the non-irrigated sectors did not exist prior to application of wastewater (Sopper and Kardos 1973).

A 100 × 100-m grid was superimposed on a map of the study area. Thirty permanent sampling points were selected randomly in forested habitat and were divided into four habitat types; types 1–3 were in the irrigated sector and type 4 was in the non-irrigated sector. Sampling points in type-1 habitat (N = 4) contained only deciduous overstory trees and were 15–40 m from an edge, points in type-2 habitat (N = 6) had a mix of deciduous and coniferous overstory trees and were 60–125 m from an edge, points in type-3 habitat (N = 14) contained only deciduous overstory trees and were 60–125 m from an edge, and points in type-4 habitat (N = 6) were reference sites with deciduous overstory trees and were 75–150 m from an edge. Sampling points in type-1, type-3, and type-4 habitats contained less than 3% coniferous overstory trees (pitch pine or white pine [*Pinus strobus*]) versus approximately 28% coniferous overstory trees in type-2 habitat (R. H. Yahner, unpubl. data). The number of points per habitat type in the irrigated sector was selected on the basis of the approximate availability of forested habitat with a given cover type and distance to an edge. An edge was defined as the interface between wooded habitat containing overstory trees and a non-wooded disturbed area (crop field, old field, or unimproved dirt road) (after Forman and Godron 1986, Yahner 1988).

The 30 points were visited six times per season from Late December to early March during two winters (1988–1989 and 1990–1991) and from late May to early July during three breeding seasons (1987, 1989, and 1991). Visits occurred between sunrise and 10:00 h, and the order of visits was randomized. At each visit, an initial 1-min equilibrium period was followed by a 5-min observation period. All birds seen or heard within a 30-m radius of the center of the point during the 5-min period were counted (DeSante 1986, Morrison

TABLE 1

TOTAL NUMBER OF CONTACTS PER FORAGING BUILD IN AN IRRIGATED AND A NON-IRRIGATED SECTOR OF A STUDY AREA ON STATE GAME LANDS 176 DURING TWO WINTERS AND THREE BREEDING SEASONS IN CENTRAL PENNSYLVANIA, 1987–1991

	Winter			Breeding			
Foraging guild	1988–1989	1989–1990	Total	1987	1989	1991	Total
Ground-shrub forager	111	91	202	209	161	324	694
Trunk-bark forager	59	67	126	26	13	21	60
Sallier-canopy forager	0	4	4	228	98	165	431

et al. 1986, Yahner 1993). The total number of contacts obtained during the six visits was pooled for each point by season (N = five, two winters and three breeding seasons) for each foraging guild (ground-shrub, trunk-bark, and sallier-canopy forager) or species (guild classifications followed those of Yahner 1986, 1993).

The total number of contacts per guild or common species (defined as a species with >20 contacts in a given season or seasons combined) was compared among the four habitat types for each of the five seasons separately, both winters combined, and the three breeding seasons combined, using *G*-tests for goodness-of-fit (Sokal and Rohlf 1981). The expected number of contacts was obtained by multiplying the proportion of total permanent sampling points per habitat type by the total number of contacts per guild or common species in a given season(s). Data were pooled between winters and among breeding seasons to give an additional measure of habitat-use patterns among habitat types and to increase sample size for statistical analyses (Rice et al. 1984, Yahner 1986). When a statistical difference in the number of contacts of a guild or a common species occurred among the four habitat types in a given season(s), a posteriori *G*-tests for goodness-of-fit were conducted about the cell (habitat type) of interest (Sokal and Rohlf 1981). Statistical differences were designated as $P < 0.05$ for all analyses.

Results.—Most contacts of wintering birds were those of ground-shrub (60.8%) and trunk-bark foragers (38.0%) (Table 1). Twenty-five bird species were observed on the study area in winters 1988–1989 and 1990–1991 combined, and approximately one-third (32.0%) of these were common species. The five most abundant species in order of decreasing total number of contacts were three trunk-bark foragers, Black-capped Chickadee (*Parus atricapillus*), Tufted Titmouse (*P. bicolor*), and Downy Woodpecker (*Picoides pubescens*) and two ground-shrub foragers, Dark-eyed Junco (*Junco hyemalis*) and White-throated Sparrow (*Zonotrichia albicollis*).

Type-1 habitat was used more than expected by ground-shrub foraging species in winter (Table 2). Species occurring more than expected in this habitat included Dark-eyed Junco, Northern Cardinal (*Cardinalis cardinalis*), and White-throated Sparrow. Type-2 habitat was used principally by trunk-bark foragers, e.g., Black-capped Chickadee, Tufted Titmouse, and Downy Woodpecker. Type-3 habitat was used in proportion to its availability in winter but tended to be preferred by Dark-eyed Juncos. Type-4 habitat was used less than expected by the wintering bird community, especially by four common species: Tufted Titmouse, Dark-eyed Junco, Northern Cardinal, and White-throated Sparrow.

More than twice as many species (N = 54) were noted on the study area in the breeding seasons during 1987, 1989, and 1991 combined as compared with winter seasons. As in winter, the major foraging guild in the breeding seasons was ground-shrub foragers (58.6%

TABLE 2

TOTAL NUMBER OF CONTACTS PER FORAGING GUILD IN FOUR HABITAT TYPES BY SEASON(S) IN AN IRRIGATED AND A NON-IRRIGATED SECTOR OF A STUDY AREA ON STATE GAME LANDS 176 IN CENTRAL PENNSYLVANIA, 1987–1991

Foraging guild[a]	Season	Habitat type			
		I	II	III	IV
Ground-shrub foragers	Winter 1988–1989	35[b]	19	46	11[c]
	Winter 1990–1991	22[b]	26	35	8[c]
	Both winters	57[b]	45	81	19[c]
	Breeding 1987	58[b]	32	83[c]	36[c]
	Breeding 1989	49[b]	33	55[c]	24
	Breeding 1991	69[b]	69	156	30[c]
	All breeding	176[b]	134	294[c]	90[c]
Trunk-bark foragers	Winter 1988–1989	10	23[b]	21	5[c]
	Winter 1990–1991	6	24[b]	27	10
	Both winters	16	47[b]	48	15
Sallier-canopy foragers	Breeding 1987	79[b]	28[c]	82[c]	39
	Breeding 1991	14	31	101[b]	19[c]
	All breeding	40[c]	83	234[c]	74

[a] Only guilds with a significant ($G \geq 7.82$, df = 3, $P < 0.05$) difference in number of contacts among habitat types in a given season(s) are given in the table.

[b] Number of contacts was significantly ($G > 3.84$, df = 1, $P < 0.05$) greater in this habitat type than in the other three types combined.

[c] Number of contacts was significantly ($G > 3.84$, df = 1, $P < 0.05$) less in this habitat type than in the other three types combined.

of total contacts) (Table 2); sallier-canopy foraging species, however, comprised the next most common foraging guild (36.4% of total contacts). About one-third (35.2%) of the breeding bird community consisted of common species. The five most abundant species based on the total number of contacts were Common Yellowthroat (*Geothypis trichas*), Red-eyed Vireo (*Vireo olivaceus*), Indigo Bunting (*Passerina cyanea*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Song Sparrow (*Melospiza melodia*). The vireo and the bunting were sallier-canopy foragers, whereas the other three were ground-shrub foragers.

As in winter, type-1 habitat was used more than expected by ground-shrub foraging species in the breeding seasons (Table 2); based on all breeding seasons combined, this habitat was avoided by sallier-canopy foragers. Species occurring more than expected in type-1 habitat were Gray Catbird (*Dumetella carolinensis*), American Redstart (*Setophaga ruticilla*), Common Yellowthroat, Common Grackle (*Quiscalus quiscula*), American Goldfinch (*Carduelis tristis*), and Song Sparrow; species less likely to occur in this habitat were Red-eyed Vireo, Ovenbird (*Seiurus aurocapillus*), Scarlet Tanager (*Piranga olivacea*), and Rufous-sided Towhee. Type-2 and type-3 habitats generally were used in proportion to their availability by the breeding bird community; however, some species, e.g., Common Yellowthroats, used these habitats more than expected, and others, e.g., Ovenbird, used these habitats less than expected. Type-4 habitat was avoided by ground-shrub foraging species, including Gray Catbird, American Redstart, Common Yellowthroat, Common Grackle, Northern Cardinal, Indigo Bunting, Rufous-sided Towhee, and Song Sparrow; only the Ovenbird used type-4 habitat more than expected.

Discussion.—The wintering bird community in my study essentially consisted of two major guilds, ground-shrub and trunk-bark foragers, each exhibiting preferential use of the different habitat types. Ground-shrub foragers, particularly Dark-eyed Juncos and White-throated Sparrows, were prevalent along forest edges (type-1 habitat), perhaps because of the availability of abundant weed seeds as a food resource (Rollfinke and Yahner 1990). In contrast, these species were absent from nearby forest stands managed by an even-aged system of clear-cutting, which were located about 10 km from the study site (i.e., Barrens Grouse Habitat Management Study Area [HMA]), because of a paucity of weed seeds in winter (Yahner 1986, 1993).

Although trunk-bark foragers, e.g., Black-capped Chickadee, Tufted Titmouse, and Downy Woodpecker formed wide-ranging interspecific flocks (Rollfinke and Yahner 1991a), this guild preferred type-2 habitat for at least two reasons. First, pitch pine in this habitat type was an important foraging substrate for trunk-bark foragers (Yahner 1987, Rollfinke and Yahner 1991b); pitch pine and other rough-barked trees have numerous crevices used as hiding places by arthropods which serve as food for wintering birds (e.g., Jackson 1979, Brawn et al. 1982). Second, compared with deciduous trees, conifers likely provided a more favorable microclimate for birds by reducing windchill and energetic costs while foraging during winter. As in nearby managed forest stands at the Barrens Grouse HMA (Yahner 1986, 1993), ground-shrub and sallier-canopy foragers in the present study were the predominant guilds during the breeding seasons. Because most ground-shrub foraging species were found in type-1 habitat and less so in type-2 and type-3 habitats of the irrigated sector, distance to a forest edge probably was a major factor influencing the distribution of this guild. Strelke and Dickson (1980) and Yahner (1987), for example, noted that many forest birds adapted to edge and brushy conditions created by forest clear-cutting typically occurred within 25 m of the forest edge; sampling points in type-1 habitat usually were located about this distance from an edge.

Another factor affecting abundance and distribution of ground-foraging species was the presence of a lush, herbaceous layer of vegetation throughout the irrigated sector on the study area. Although several ground-foraging species in my study are considered edge species, such as Gray Catbird and Common Yellowthroat, and typically occupy habitat with dense understory vegetation (e.g., Forman et al. 1976; Whitcomb et al. 1981; Yahner 1991, 1993), they were relatively abundant throughout the irrigated sector (types 1–3) not only in type-1 habitat but also in types 2 and 3. Conversely, these species were scarce or absent in type-4 habitat which lacked a dense layer of herbaceous vegetation near ground level. On the other hand, one ground-shrub foraging species, the Ovenbird, was characteristic of type-4 habitat, probably because of reduced herbaceous growth. The Ovenbird is principally a forest-interior species (see Whitcomb et al. 1981, Yahner 1993), but while foraging it utilizes forest floors that lack abundant herbaceous cover (e.g., see Kahl et al. 1985, Holmes and Robinson 1988, Mulvihill 1992). Therefore, my findings suggest that the Ovenbird was the only species whose distribution and relative abundance were affected detrimentally by wastewater irrigation (see also Lewis and Sampson 1981, Rollfinke and Yahner 1990). In addition, a previous study found that Wood Thrushes (*Hylocichla mustelina*) were affected negatively by irrigation because dense herbaceous vegetation near ground level likely reduced foraging efficiency (Rollfinke et al. 1990). Sallier-canopy foraging species, such as Red-eyed Vireo and Scarlet Tanager, tended to favor habitat types away from forest edges (types 2–4) in my study because these species typically are area-dependent, forest-interior species (Whitcomb et al. 1981, Robbins et al. 1989).

Acknowledgments.—This study was supported by the Pennsylvania Agricultural Experiment Station and the Max McGraw Wildlife Foundation. I thank B. Balcom for reviewing

the manuscript, and B. Burhans, J. Gillis, G. Hennemuth, B. Plowman, J. Puschock, B. Rollfinke, B. Ross, and S. Werner for field assistance.

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Wilson Bull., 107(2), 1995, pp. 371–373

Sequence of plumage evolution in the Standardwing Bird of Paradise.—The faded appearance of the plumage of the Standardwing Bird of Paradise (*Semioptera wallacii*), endemic to Halmahera and Bacan (Batjan) Islands (White and Bruce 1985), is unique within the Paradisaeidae. The dull, unbarred plumage of both sexes is primarily medium brown, darker on the mantle, fading to a pale buffy-white on the remiges (see Gilliard 1969, Cooper and Forshaw 1977). Males possess an iridescent green breast shield and a pair of remarkable elongated wing coverts on each wing. These plumage elaborations have long attracted the attention of ornithologists, while the remainder of the plumage, arguably more interesting in an evolutionary sense, has largely been ignored until Frith (1992).

The phylogenetic relationships of *Semioptera,* a monotypic genus, are poorly known and in dispute. Nearly two-thirds of the fifteen currently recognized genera in the Paradisaeidae (Beehler and Finch 1985, White and Bruce 1985) have been suggested as possible sister taxa of *Semioptera* by taxonomists (see Frith 1992). Given the incredible variety of plumages within this assemblage of genera, especially among males, it is not possible at this time to determine the plumage color and pattern of its ancestor. Nevertheless, several lines of evi-

dence suggest that *Semioptera*'s plumage is aberrant and that the plumage of ancestral populations was predominately black or dark brown.

I examined series of museum skins of *Semioptera* (20+) and all other birds of paradise in the American Museum of Natural History and the National Museum of Natural History (USNM), Smithsonian Institution. Several feathers of one male *Semioptera* (USNM) were sectioned (12 μm) for microscopic examination.

In males of both subspecies, *Semioptera w. wallacii* and *S. w. halmaherae,* the pale grayish-brown crown has plush-like texture. Barbules are macroscopically modified for iridescent refraction but exhibit little structural color at any angle of inspection. Distal barbules (under 430× magnification) consist of a strip of flattened rectangular cells that widen distally without any differentiation into base and pennulum. A few melanin granules or granule vacuoles are scattered within each cell. Barbule flattening is a consistent feature of iridescent feathers (Lucas and Stettenheim 1972).

The intensity of iridescent scaling below the pectoral shield of male *Semioptera* is subdued owing to moderate concentrations of melanin in barbules. In contrast, the strikingly iridescent feathers of predominately black or dark brown birds of paradise (e.g., *Ptiloris* sp., *Parotia* sp., *Lophorina superba, Astrapia nigra*) possess densely pigmented barbule cells (pers. obs.).

With the exception of the adult male's white wing standards, the outer primaries are the palest part of the plumage in both sexes of *Semioptera.* The transition in melanization is gradual from the outermost to innermost remex. The rachises and barb rami of all contour feathers are pale-buffy white to white. Contrast between the distal and proximal ends of contour feathers is less than in possible sister taxa. Likewise, the contrast between dorsal and ventral plumage, countershading (Thayer 1896), is minimal in both sexes of *Semioptera.* Additionally, concentrations of melanin are low in the keratinized soft parts (Cooper and Forshaw 1977). By comparison, the rachises and webs of primaries are heavily pigmented with melanins in other birds of paradise, particularly at the tips, probably as an adaptation to reduce abrasion and wear (Burtt 1981). In sum, the absence of heavy melanization of the plumage and softparts in both sexes of *Semioptera* suggests a common genetic cause and a derived condition.

The aberrant plumage of *Semioptera* may be due to one of two possible genetic mutations. One possibility is a fixed non-eumelanic schizochroism (Buckley 1982), producing a "fawn variant." In other words, the pigment that produces black coloration (eumelanin) is absent, leaving only residual phaeomelanins, which impart a warm brown color to *Semioptera*'s plumage. The second possibility is that the density of one or several pigments has been uniformly diluted. Examples of "faded" plumage, possibly due to schizochroism or dilution, have been reported in the bird of paradise species *Cnemophilus loriae* (Frith 1987) and *C. macgregorii* (Frith and Harrison 1989). Whatever the underlying cause of *Semioptera*'s faded appearance, it appears to be genetically fixed.

Although the genetics of plumage coloration in wild birds is poorly understood, inheritance of schizochroism is recessive in several well-studied cagebirds (Buckley 1982). The morphology and color of avian plumage may be encoded by dozens or hundreds of genes. However, schizochroic mutations might involve a single regulatory gene, for instance, an inhibitor of the enzyme tyrosinase, which is necessary for melanin synthesis. In any event, it would seem that many more genes are involved in encoding the complex ultrastructure of *Semioptera*'s crown feathers than in their pigmentation. The peculiar condition of pigmentation in *Semioptera* appears to be unique as a species-specific characteristic within the Paradisaeidae.

Island isolation and the absence of other polygynous birds of paradise may have permitted a relaxation of plumage stereotypy in the ancestral population of *Semioptera.* In a lek breed-

ing system, a pale-winged mutation might have been rapidly fixed by sexual selection. The development of leucistic wing standards may also be linked to the mutation. Corresponding plumage patterns in females are probably caused by correlated selective responses between the sexes (Lande 1980). Frith (1992) concluded that the whitish primaries of *Semioptera* were as important a component in the aerial display of lekking male *Semioptera* as the breast shield and wing standards. Wing tips are also fluttered, vibrated, and spread during the wing standard display. In fact, sexual selection for contrasting visibility of the primaries and wing standards in males may be driving progressive leucism in *Semioptera.* If true, the iridescence of the heavily melanized crown feathers in ancestral populations may have been degraded by the emergence of a more sexually favored leucistic trait in descendent populations. Because the two subspecies differ only slightly in the degree of crown iridescence, the mutation resulting in their faded appearance undoubtedly occurred in the founder population before separation and differentiation on Halmahera and its land-bridge island, Bacan.

Acknowledgments.—I thank Helen Wimer for sectioning feathers, Bruce Beehler, Alan Brush, Joel Cracraft, Clifford Frith, Mary LeCroy, Kenneth Parkes, Steven Pruett-Jones, Peter Stettenheim, and Richard Zusi for helpful comments and discussion, and Mary LeCroy for permission to examine the American Museum specimens. Museum studies were supported by grants from the Smithsonian Research Opportunities Fund and the Frank M. Chapman Fund of the American Museum of Natural History.

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Wilson Bull., 107(2), 1995, pp. 374–376

Roosting behavior of Prothonotary Warblers in the non-breeding season.—Many birds aggregate and form communal nighttime roosts during nonbreeding periods. Morton (1980) found evidence suggesting that Prothonotary Warblers (*Protonotaria citrea*) roost communally in Panama. This was considered unusual, since migrant parulid warblers roost solitarily and even defend their nighttime roost positions against entry by other individuals (Morton 1980). This note provides additional information on roosting behavior in Prothonotary Warblers, based on two new data sets obtained during studies of wintering warblers in Panama and Costa Rica.

Over two seasons at a study site in Tivivies, Puntarenas, Costa Rica (November 1990 through March 1991 and November 1991 through February 1992), Prothonotary Warblers were observed moving singly and in groups between a mangrove forest, where they roosted at night, and the adjacent hillside where they foraged during the day. Data were collected here because the dryland forest configuration concentrated passerines within a narrow area. Second-growth forest on the hillside had been allowed to grow back so that it formed a wedge of habitat decreasing in width from the upper slope down to the mangrove edge, where it was about only 15 m wide and bordered on either side by open cattle pasture. Data were collected by a single observer for half-hour periods after sunrise and before sunset, every day from the end of November to the middle of January during the second winter season. The total number of Prothonotary Warblers moving past the observation point in a given half-hour observation period varied from 50 to 115 individuals (median = 70; mean $\pm$ SD = 72 $\pm$ 18; N = 68). Other species (Northern Orioles [*Icterus galbula*] Yellow-crowned Euphonias [*Euphonia luteicapilla*], Masked Tityra [*Tityra semifasciata*], Yellow-throated Vireo [*Vireo flavifrons*], White-lored Gnatcatcher [*Polioptila albilorus*], and Tennessee Warbler [*Vermivora peregrina*]) were seen moving past the point at the same time, but Prothonotary Warblers were the only species observed flying in groups of three or more.

Observations also were made at a second-growth stand of trees on Far Fan Road, adjacent to the Pan American Highway, southeast of Panama City, Republic of Panama. On 10 December 1973 and 11 January 1974, Prothonotary Warblers were observed near dusk gathering in and around an isolated roadside tree about 8 m tall and covered with vines. The tree was surrounded by a grassy area and located directly opposite the Balboa Gun Club. The warblers arrived at this pre-roost staging tree singly and in small groups. Eventually they flew off as a flock, after it became too dark to follow them visually, in the direction of a row of *Casuarina* trees at the Balboa Gun Club. Flocks of 12 or more Prothonotary Warblers were seen foraging in the Far Fan Road area at various times of the day on a regular basis during this same year.

Seventeen years later, on 20 February 1991, Prothonotary Warblers were seen staging in the same tree as during the previous observation. In three searches during that day, no warblers were seen foraging within an area extending several hundred meters from the staging tree. Loss of vegetation, in comparison with that previously present, was noted for the surrounding habitat. With assistance from three additional people, we monitored this location prior to dusk that evening. From 17:00 to 18:00 h EST, ten Prothonotary Warblers were seen moving about in the area, perching from one to 6 m up on the staging tree and eventually gathering in a nearby grove of *Luehea* trees. Among the individuals seen were males and females, adult and second-year birds. Up to the time of their departure for the roost, some warblers continued to forage in low shrubs and trees but at decreased frequencies relative to that of normal daytime foraging. At 18:10 h, roughly 20 min past sunset, eight birds were seen moving away from the staging area in a group, by 18:18 h this group appeared to split up into at least two smaller flocks. They flew the same direction from the

staging area towards the Balboa Gun Club as had the birds observed in 1973–1974, but we were unable to follow them to the exact roost site due to darkness. On driving over to the gun club, we found a large number of Great-tailed Grackles (*Quiscalus mexicanus*) and Clay-colored Robins (*Turdus grayii*) gathering in a row of *Casuarina* trees where they were roosting. It was unclear whether or not the warblers joined this larger aggregation.

Explanations of communal roosting behavior have revolved around thermoregulatory arguments (e.g., Chaplin 1982), predator protection (e.g., Hamilton et al. 1967), and the transfer of foraging information (e.g., Ward and Zahavi 1973; but see also Mock et al. 1988). Based on our observations of Prothonotary Warblers, we suggest that a scarcity of suitable roosting sites also may lead to such behavior. Differences in roosting requirements from other warbler species could be related to the fact that, aside from the Lucy's Warbler, no other parulid warbler except the Prothonotary is a cavity nester. If the Prothonotary Warbler does indeed have very specific roost-site requirements which only certain trees provide, association between yearling and adult birds during day-time periods may be essential to the transfer of locational information and the continued survival of populations. Du Plessis and Williams (1994) have made similar arguments concerning the social behavior of Green Woodhoopoes (*Phoeniculus purpureus*). They suggested that a shortage of suitable cavity roosts (in conjunction with an apparent physiological intolerance for even moderately low nighttime temperatures; Ligon and Ligon 1978) has lead to the evolution of conspecific group living among Green Woodhoopoes.

Typically, the Prothonotary Warblers seen moving to and from roosting areas flew rapidly from perch to perch, using frequently repeated "seep" calls as if to maintain contact with group members. This behavior was similar to that reported for migrants moving to roosts in Puerto Rico by Staicer (1992). During our observations, we also noted that Prothonotary Warblers began to tail fan more frequently while perched, as light levels decreased near dusk. Fanning the tail feathers exposes white patches on the inner webs of the outer rectrices; these patches are more prominent in adult than yearling birds (Pyle et al. 1987). Some individuals held the tail feathers open for periods up to 10 sec, perhaps using the behavior as an additional signal to maintain contact with other members of the flock while moving to a roost.

Within the two field seasons completed in Costa Rica, eight (of 60) color-banded individuals (that had been marked at hillside trapping stations as much as four weeks prior to roosting observations) were seen moving between the hillside and mangrove on up to three occasions per individual. One Prothonotary trapped in 1990–1991 on the hillside was seen moving into the mangrove at dusk the following season. Although limited in number, these observations suggest consistent use of the same pathway between roosting and foraging sites for at least part of the non-breeding season and possibly between years. Similar observations of large numbers of Prothonotary Warblers moving together at dusk have been recorded for Playa Honda, Panama (letter from Horace Loftin to Alexander Wetmore dated 21 December 1966).

Prothonotary Warblers forage solitarily, in pairs, as well as in mixed- and single-species flocks (Morton 1980; Warkentin, unpubl. data). Of 502 foraging Prothonotary Warblers encountered over two seasons (dates listed above) in Costa Rica, only 14% (69 individuals) were seen foraging alone. The remainder of these birds were either in mixed- (191 birds in 50 groups) or single-species (242 birds in 55 groups) flocks, with a mean of 2.8 and 3.4 other conspecifics in the flock, respectively. The use of communal roosts may have implications for the development of sociality in this species. If suitable roosting sites for this species are rare in the habitat, joining flocks during the day which contain other Prothonotary Warblers may be a means of discovering the location of scarce, suitable roost sites. The majority of individuals seen foraging alone were adults; yearlings, which were at least

initially unfamiliar with their wintering habitat, tended to be found only in association with other Prothonotary Warblers throughout the winter (Morton 1980; Warkentin, unpubl. data). Information on, and quantitative measures of, actual sites used for roosts by Prothonotary Warblers are essential to furthering our understanding of this behavior.

Acknowledgments.—We thank Kim Derrickson, Tom Parsons, and Storrs Olson, for helping make the 1991 observations in Panama, Ricardo Portugues for assisting in Costa Rica. Funding to Ian Warkentin was provided by the Natural Sciences and Engineering Research Council of Canada, Smithsonian Migratory Bird Center, and North American Bluebird Society. Dennis Murphy and the Center for Conservation Biology of Stanford University provided logistical support during preparation of the manuscript. Gene Morton received support through grants from the National Geographic Society and the Smithsonian Institution Scholarly Studies Program (#1235 S909). Allan Keast commented on an earlier version of this note.

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Wilson Bull., 107(2), 1995, pp. 377–379

Time of day of egg laying by Eastern Bluebirds.—The time of egg laying varies among species. Most passerines lay their eggs shortly after sunrise, but several species lay their eggs well after sunrise (Schifferli 1979). The time of egg laying is known accurately for relatively few species, partly due to the difficulty in determining when it occurs. An accurate assessment of the time of egg laying can be important for studies of reproductive strategies. In most passerines, eggs are fertilized at 24-h intervals, and the next egg in a sequence is fertilized in the hour after the laying of the previous egg. The time of egg laying thus indicates the time of fertilization. In species with sperm competition (Birkhead and Møller 1992), this hour after egg laying should be the optimal time for copulation attempts, because inseminations will be most likely to fertilize the next egg. Consequently, this will also be a critical time for mate guarding by males against extra-pair mating attempts. We report here an estimate of the time of day of egg laying in Eastern Bluebirds (*Sialia sialis*) using the method developed by Scott (1993) to analyze data we collected during a study of mate guarding (Meek and Robertson 1994).

Methods.—We studied Eastern Bluebirds breeding in nest boxes near the Queen's University Biological Station, Chaffeys Locks, Ontario (44°34′N, 76°19′W), from April to July, 1989 and 1990. Most birds were unbanded at the start of this study, because we usually captured bluebirds in the nestbox during late incubation or shortly after the young hatched. As part of a study on mate guarding, we observed the behavior of Eastern Bluebird pairs before and during the egg-laying period. We made half-hour nest observations between 04:30 and 10:30 h (EST). Following a nest observation, we checked the nest contents if we knew that the female was not in the box. In addition, we made regular checks of focal and non-focal nests after 12:00. In this way, we obtained 145 "nest check" observations during egg laying from 56 different females. All observations in this study were made between April 8 and May 10 on females laying their first clutches.

Each time we visited a nest, we recorded the time of day and the presence or absence of new eggs in the nest. We assume that female Eastern Bluebirds lay their eggs at 24-h intervals, as is typical of passerines. The observations were categorized according to whether a new egg was present or absent and grouped into 1-h time intervals. For each time interval, we calculated the proportion of nests containing a new egg. At the medium time of the daily egg-laying period, the proportion of nests containing a new egg changes from <50% to >50%. We then tested whether there was a significant change in the proportion of nests containing a new egg between the two time intervals adjacent to the interval in which about 50% of eggs were laid. Further details of the logical basis and procedures of this method are in Scott (1993). We report all times as Eastern Standard Time (EST).

Results.—No new eggs were laid before 0:630 EST (N = 26 observations). A few eggs were laid before 07:00, and most new eggs were present by 09:00 (Table 1). Only three eggs were laid after 09:00. Hence, the daily laying period spanned about 2.5 hours, from 06:30 to 09:00. The proportion of nests containing a new egg changed significantly from 19% (4/21) between 06:01–07:00 to 86% (18/21) between 08:01–09:00 (G-test, $G_{adj} = 9.87$, $P < 0.005$). The proportion of nests with a new egg reached 50% between 07:01 and 08:00 (Table 1). Hence, we estimate that the mid-point of this hour, 07:30, was close to the median laying time for Eastern Bluebirds in eastern Ontario.

Discussion.—Eastern Bluebirds have been reported to lay their eggs around 08:00 EST in Ithaca, New York (Hamilton 1943), and about 2 h after sunrise at 08:30 in Arkansas (Thomas 1946). Our results agree with those observations. Sunrise in eastern Ontario is around 05:30 (EST) in April and 05:00 in early May (Weatherhead et al. 1991). All female

TABLE 1

THE NUMBER AND PERCENTAGE OF TIMES THAT A NEW EGG WAS PRESENT AT THE TIME OF THE OBSERVER'S VISIT TO AN EASTERN BLUEBIRD NEST

Time of visit (EST)	New egg		Percent of nests (N) with new egg
	Present	Not present	
05:01–06:00	0	16	0% (0/16)
06:01–07:00	4	17	19% (4/21)
07:01–08:00	13	12	52% (13/25)
08:01–09:00	18	3	86% (18/21)
09:01–10:00	22	2	92% (22/24)
10:01–11:00	11	1	92% (11/12)
After 12:00	26	0	100% (26/26)

Eastern Bluebirds laid their eggs after 06:30, at least one hour after sunrise, and the median time of egg laying (07:30) was around two hours after sunrise.

The timing of egg laying varies considerably among species. For example Red-winged Blackbirds (*Agelaius phoeniceus*) lay shortly after sunrise, 04:37–0:601 EST (Muma 1986). Female Tree Swallows (*Tachycineta bicolor*) lay their eggs between 05:20 and 07:05 EST, or 05:57 on average (Venier and Robertson 1991). In Gray Catbirds (*Dumetella carolinensis*) the median time of egg laying is 07:00 EST, about two hours after sunrise (Scott 1993), and in American Robins (*Turdus migratorius*), a member of the same family (Turdidae) as Eastern Bluebirds, the average time of egg laying is 10:32 EST (Weatherhead et al. 1991).

The question of what time of day female birds should lay their eggs has not been frequently addressed. As a result, only a few hypotheses regarding when a female should lay her eggs have been proposed. Schifferli (1979) suggested that females lay early in the morning to minimize constraints on their activity. Because eggs are most vulnerable to destruction late in development, if females lay early in the morning, the eggs are most vulnerable at night when females are inactive anyway (Schifferli 1979). However, having an egg in the oviduct does not constrain activity of female American Robins (Weatherhead et al. 1991). Weatherhead et al. (1991) suggested that the timing of egg laying may result from selection on the optimal timing of fertilization or on the best time for copulations. Recently, Scott (1991) examined whether egg laying before sunrise by female Brown-headed Cowbirds (*Molothrus ater*) was a specialization for brood parasitism. Female Brown-headed Cowbirds lay their eggs on average 9 min before sunrise, whereas seven potential host species all lay their eggs after sunrise (Scott 1991). laying before sunrise may be advantageous to female cowbirds, but there are insufficient data on other icterines to assess whether early laying arose as an adaptation to brood parasitism (Scott 1991). Finally, foraging strategies may influence the timing of laying. Aerial insectivores such as Tree Swallows must spend considerable time in flight and should oviposit early in the morning, both to increase their flying efficiency during the day and because foraging probably improves with time of day as the temperature increases and insects become more active. Species such as Eastern Bluebirds or American Robins which forage on the ground or from a perch do not need to fly as much, and holding an egg is probably of little consequence to foraging efficiency. These hypotheses have not yet been adequately tested, and there may be other equally plausible hypotheses that explain the timing of egg laying in birds. Most likely the timing of egg laying will be influenced by different factors in different species.

Acknowledgments.—We thank Caroline Tomlin for assisting with the field work, and David Scott and an anonymous reviewer for their reviews. The Queen's University Biological Station provided logistical support. Funding was provided by the Natural Sciences and Engineering Research Council of Canada, the Canadian Wildlife Service, the North American Bluebird Society, and the Animal Behavior Society.

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Wilson Bull., 107(2), 1995, pp. 379–382

Sex-biased kleptoparasitism of Hooded Mergansers by Ring-billed Gulls.—Kleptoparasitism is common in many seabirds (Furness 1987; Duffy 1980, 1982), including gulls (Grace 1980, Spear and Ainley 1993). In Laridae, 23 of 88 species have been reported to be kleptoparasites (Brockman and Barnard 1979). Among *Larus* gulls differences in kleptoparasitism of conspecifics and other gull species appears to be related to age, with young being pirated more often (Burger and Gochfeld 1981). Some parasitic seabirds may attack certain hosts while ignoring others (Spear and Ainley 1993). Selective kleptoparasitism appears to be related to host species' size and relative abundance (Spear and Ainley 1993), and age and experience of the pirate (Burger and Gochfeld 1981). I could not locate a reference where the parasitic species has shown a consistent preference for attacking one sex over the other of the same species. Here I report on observations of Ring-billed Gulls (*Larus delawarensis*) differentially kleptoparasitizing male and female Hooded Mergansers (*Lophodytes cucullatus*) feeding in a saltwater pond in the coastal saltmarsh of Aransas National Wildlife Refuge, in the coastal region of Texas in Refugio and Calhoun counties, approximately 65 km north of Corpus Christi.

TABLE 1

VISIBLE PREY CAPTURE RATES OF HOODED MERGANSERS AND NUMBER OF PARASITIC ATTACKS BY RING-BILLED GULLS AT A COASTAL SALTMARSH POND ON THE TEXAS COAST

Sex	Number of dives	Captures		Gull attacks		Prey theft	
		Total	%	Total	%	Total	%
Males	97	6	6	0		0	
	78	4	5	0		0	
	68	2	3	0		0	
	82	4	5	0		0	
Total	325	16	5	0	0	0	0
Females	79	3	4	2	66	1	50
	46	2	4	2	100	1	50
	34	1	3	1	100	1	100
	49	2	4	2	100	1	50
Total	208	8	4	7	88	4	57

In Texas, Ring-billed Gulls are abundant in winter along the coast and are known to rob food from several gull species (Payne and Howe 1976) and other water birds, particularly ducks, and they commonly parasitize diving and fish-eating duck species. No information on kleptoparasitism of Hooded Mergansers by Ring-billed Gulls is available.

During two days of observation, three (15 November) and one (16 November) pairs of Hooded Mergansers were foraging in a pond 20–50 m away from my blind. Water depth of the pond varied from 30–40 cm. On both days there was a Ring-billed Gull that followed (by swimming) a foraging pair of mergansers and was present the entire time there was any feeding activity by mergansers. The gull apparently followed the mergansers visually while they were underwater for at least one of the pair of ducks, usually the female, would emerge close (<1 m) to the gull after surfacing from a dive. After a successful capture by a female merganser, the gull would take flight and commence harassing the duck with prey. All prey captured by both sexes and brought to the surface consisted of small fish of unknown species. It is not known if it was the same gull following the mergansers on both days. At least three other Ring-billed Gulls joined the first gull in attacking the ducks but were present only for a few minutes after which they flew out of sight. The gull following the mergansers made no attempts to capture prey on its own the entire time it was watched.

During my observations, I followed the foraging activity of the pair of mergansers which the gull was following at the time. I recorded the number of dives by each sex and noted whether a prey item was captured and brought to the surface. After a successful dive by a merganser, the behavior of the Ring-billed Gull was noted as an attack on the merganser if it flew towards the duck and displayed aggression. I then noted whether the gull successfully robbed the merganser of its captured prey.

The Ring-billed Gull differentially parasitized the sexes of the mergansers, selecting females disproportionally (Table 1). Foraging males were never attacked despite their capturing twice as many visible prey (Table 1) as females. The females, however, were attacked 88% of the time after a prey capture. A single incidence was observed of a directed flight of a gull toward one of the males after a successful dive. On this occasion the gull flew toward the male after it surfaced with prey; however, the gull stopped short and did not

attack, landing close to the male merganser. The male merganser made no effort to evade the gull as it flew toward it and merely stood its ground. In contrast, upon approach of a gull, females with prey dove or swam away from the gull which persistently chased a swimming bird or fluttered above the water waiting for a female to resurface after a dive. All observed attacks on females lasted less than one min and ended in release of prey or, less often, in consumption of prey by the female merganser. The gulls were successful in robbing the female mergansers of their prey 57% of the times they attacked.

The reasons for preferential parasitism of female Hooded Mergansers by Ring-billed Gulls are unknown. The sexes of the Hooded Merganser and other mergansers show only minor differences in size and weight (Bellrose 1980) but show striking sexual dimorphism in coloration. Since males and females were present in equal numbers during the entire time my observations took place, there was no local density dependent factor that may account for the gulls' differential attack on females. Lamore (1953) noted, over several weeks, that there were no Ring-billed Gull attacks on Common Mergansers (*Mergus merganser*) while both females and males were present in a reservoir in Washington D.C., but he saw repeated attacks and robbing of prey on females once males were no longer present in the reservoir. The reason for the behavior observed by Lamore is unexplained. Grace (1980) showed that Ring-billed Gulls attacked female Common Mergansers 12 times and males only once; however, there is no information regarding the number of each sex present at the time of the attacks.

Differential attacks on the sexes are unlikely to be related to sexual differences in prey capture success rates of the host. Male mergansers had greater prey capture rates, yet were not attacked. It is possible that female Hooded Mergansers are more susceptible to attack because of their behavioral response upon an imminent attack by a gull. If males stand their ground upon approach by a gull, as was observed, it may serve as a cue for the potential parasite that the prey will not be given up. Females may be more likely to be attacked because of their response to approaching gulls. Female mergansers may be more likely to give up prey or release prey with less harassment than males; therefore, it would be more profitable for a gull to expend energy attacking a female despite her lower prey capture success rate.

Acknowledgments.—I thank Jerrad Van'T Hull and Tom V. Stehn for comments on earlier drafts of this manuscript.

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Wilson Bull., 107(2), 1995, pp. 382–387

Intraspecific variation in egg composition.—Intraspecific egg composition may vary depending upon the size of the egg (e.g., Ricklefs 1977, 1984; Boersma 1982; Birkhead and Nettleship 1984; Alisauskas 1986; Hepp et al. 1987; Rohwer 1986; Hill 1988; Arnold et al. 1991). Statistical techniques derived from allometry (the study of size and its consequences) customarily are used to examine the relation between egg size and egg composition (Reiss 1989). Typically, the log of egg component mass, such as wet albumen, is regressed on the log of egg mass ($\log[y] = \log[a] + b \log[x]$). The slopes of these functions (b) depict the rate at which the egg component varies with egg size. When the slope of a log-log function is equal to 1.0 (isometry), increases in egg size are accompanied by proportionate increases in the particular egg component; consequently, the percentage of egg component will remain constant across eggs of different sizes. Slopes greater than 1.0 (positive allometry) indicate that the component mass increases disproportionately with increases in egg mass; accordingly, large eggs will contain proportionately more component mass than will small eggs. Conversely, slopes less than 1.0 (negative allometry) demonstrate that components increase proportionately less than egg mass, so that large eggs will consist of relatively smaller amounts of the egg component.

Investigations of the allometric relation between egg components and egg size have yielded some apparent differences between altricial and precocial birds. For example, Ricklefs (1984) found for the altricial European Starling (*Sturnus vulgaris*) that albumen content varied isometrically with egg mass, whereas both yolk and lipid mass displayed negative allometry. Hence, the percentage of albumen remained more or less constant in eggs of different sizes, but the percentage of yolk and lipid decreased with increasing egg size. In contrast, Ankney (1980) demonstrated for the precocial Lesser Snow Goose (*Chen caerulescens*) that both albumen and yolk varied isometrically with egg size. To determine the generality of these findings a comparative analysis, using the published data on egg composition allometry, was conducted. The purpose of the present study was to ascertain whether differences exist between altricial and precocial birds with respect to the allometric variation of egg composition.

Methods.—I compiled data from 31 species in 16 families (a summary of species and sources is available from the author). For each species I noted the slope (b) of the allometric (log-log) functions for wet albumen mass, dry albumen mass, wet yolk mass, dry yolk mass, and lipid mass (y variables) regressed on egg mass (x). The general category of development for the species, altricial or precocial, was also recorded (Nice 1962). Because there is disagreement regarding the developmental classification of pelagic-feeding seabirds, I did not include them in the overall analysis (3 families) and present their data separately. The main

TABLE 1

MEAN (± SE) ALLOMETRIC VARIATION[a] OF EGG COMPOSITION FOR ALTRICIAL AND PRECOCIAL FAMILIES

Allometric function	Precocial	Altricial	t^b	P^c
Wet albumen	1.04 (0.06)	1.21 (0.04)	2.68	0.02
	N = 6	N = 5		
Dry albumen	1.02 (0.05)	1.16 (0.09)	1.33	0.23
	N = 5	N = 4		
Wet yolk	0.90 (0.09)	0.57 (0.09)	2.64	0.03
	N = 7	N = 4		
Dry yolk	0.90 (0.15)	0.62 (0.08)	1.67	0.15
	N = 5	N = 4		
Lipid	0.81 (0.16)	0.69 (0.10)	0.64	0.55
	N = 4	N = 4		

[a] Slope of log(egg component) regressed on log(egg mass).
[b] Independent *t*-tests.
[c] Two-tailed *P* values.

data set contained information from seven precocial families and six altricial families. Due to the limited number of families, I did not further divide the data set into finer developmental classifications (e.g., semi-precocial, semi-altricial). Seven families (Apterygidae, Phasianidae, Sulidae, Pellecanidae, Corvidae, Sturnidae, Tyrannidae) had data from only one species as the family representative. Analyses were repeated using the species as independent data points and, notably, all of my results were consistent, regardless of whether species or family was the unit of analysis.

Sample sizes differed across the component variables because some measurements (e.g., dry masses and lipid mass) were not taken in the original studies. To test for differences between altricial and precocial families, *t*-tests were conducted on the allometric functions for the various egg components. Isometry was determined by *t*-tests comparing the data for precocial or altricial families to a population mean of 1.00; significant differences indicated either positive (>1) or negative allometry (<1), depending upon the particular mean value. Standard deviates (*z*-scores), within each developmental category, were calculated by using the mean and standard deviation corresponding to that group. These standard deviates were examined to determine the degree of departure from the group average for families within each of the two developmental categories.

Results and discussion.—The allometric functions for two egg components differed significantly between precocial and altricial families (Table 1): wet albumen *b* was significantly larger for altricial species whereas wet yolk *b* was significantly larger for precocial species. The mean slope for altricial families indicates positive allometry for wet albumen ($t = 5.27$, $df = 4$, $P < 0.01$), so that increases in egg size for these birds would be associated with disproportionate increases in albumen. In contrast, wet yolk ($t = -4.79$, $df = 3$, $P < 0.05$) and dry yolk ($t = -4.62$, $df = 3$, $P < 0.05$) display negative allometry for altricial birds. In addition, there was a trend for lipid to display negative allometry for altricial birds ($t = -3.11$, $df = 3$, $P = 0.053$). Yolk mass (wet and dry), albumen mass (wet and dry), and lipid mass increased isometrically with egg size in precocial species. Data from the five pelagic-feeding species (Table 2) show positive allometry for albumen and negative allometry for yolk, thus reflecting a pattern more similar to altricial species.

TABLE 2

ALLOMETRIC VARIATION[a] OF EGG COMPONENTS FOR PELAGIC-FEEDING BIRDS

Family	Species	Wet albumen	Dry albumen	Wet yolk	Dry yolk	Reference
Hydrobatidae	*Oceanodroma furcata*	1.65	—	0.05	—	Boersma, 1981
	O. leucorhoa	0.72	0.44	0.65	0.52	Montevecchi et al., 1983
Procellariidae	*Puffinus griseus*	1.35	—	0.46	—	Warham, 1983
	P. tenuirostris	1.20	—	0.67	—	Meathrel et al., 1993
Diomedeidae	*Diomedea immutabilis*	1.27	—	0.58	—	Warham, 1983

[a] Slope of log(egg component) regressed on log(egg mass).

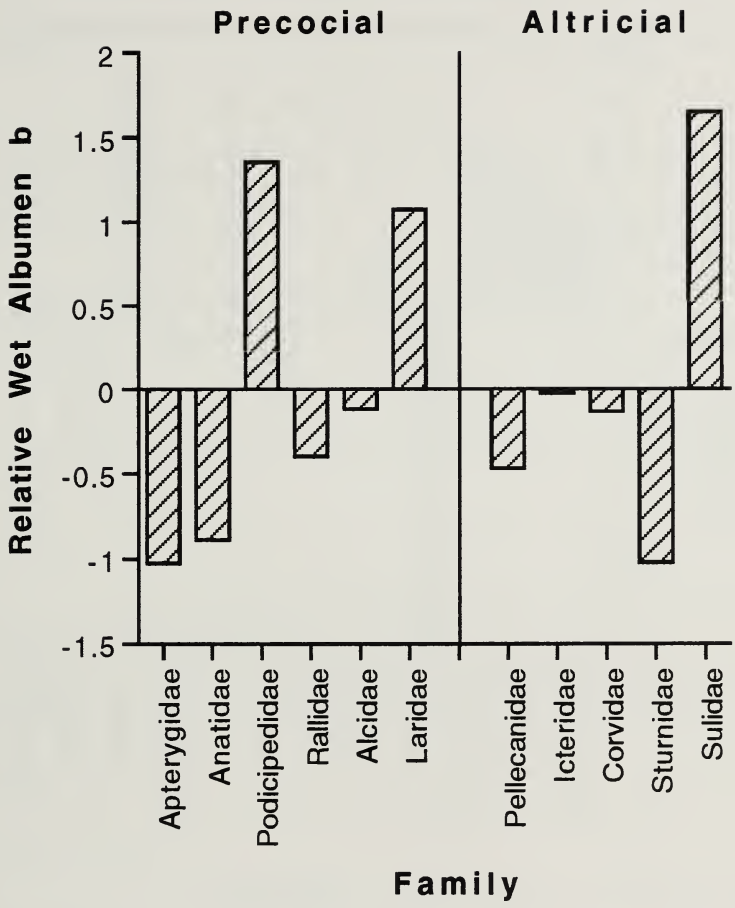

FIG. 1. Relative wet albumen *b* (z-scores) for precocial and for altricial families.

Standard deviates of the allometric functions for wet albumen and for wet yolk indicate that the Podicipedidae family tends not to follow predicted patterns for precocial species (Figs. 1 and 2). Although grebes are classified as precocial 4 (Nice 1962), the intraspecific variation of their egg components was more similar to the pattern characteristic of altricial families and pelagic-feeding birds. For example, albumen increased at a greater rate than egg size (wet albumen $b = 1.23$; dry albumen $b = 1.24$) whereas the proportion of yolk decreased with increases in egg size (wet yolk $b = 0.43$; dry yolk $b = 0.44$). Indeed, for each of these egg component functions, the Podicipedidae had the largest standard deviates among all the precocial families. Among altricial families for wet albumen (Fig. 1), the Sulidae had the largest standard deviate, in this case indicating that the slope of their allometric function for wet albumen ($b = 1.36$) was greater than typical for altricial species. The Icteridae had the largest standard deviate for wet yolk allometry (Fig. 2) in that they demonstrated a more isometric pattern than typical for altricial species (wet yolk $b = 0.81$).

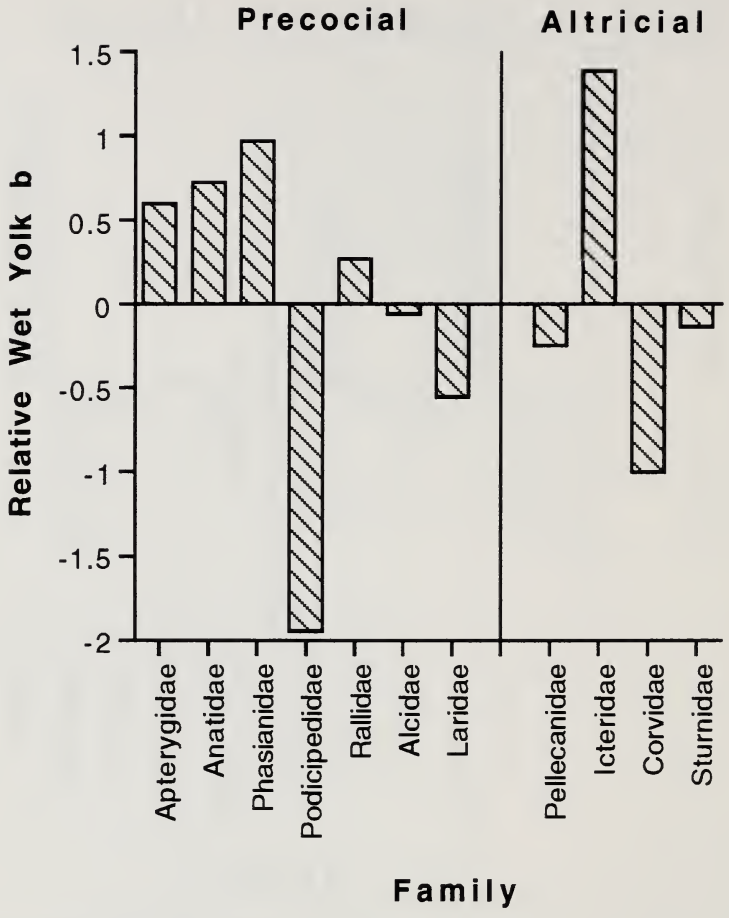

FIG. 2. Relative wet yolk *b* (z-scores) for precocial and for altricial families.

It remains to be determined whether these allometric patterns correspond to unique adaptations between altricial and precocial birds. Because variation in egg composition within species can affect the developmental characteristics of chicks (e.g., Hill 1993, Sotherland et al. 1990), it is possible that altricial chicks from different-sized eggs might show contrasting developmental patterns. For precocial chicks, however, because egg composition varies isometrically no such size effects would generally be expected. It is suggested that researchers examine the potential impact of these allometric patterns for the ontogeny of chicks from different developmental modes.

Acknowledgments.—T. W. Arnold, W. M. Hochachka, and J. A. Horsfall graciously provided unpublished data on *Xanthocephalus xanthocephalus, Pica pica* and *Fulica atra,* respectively. A. J. Vinchur provided statistical advice. W. A. Calder, J. A. Horsfall, T. J. Jackson, R. E. Ricklefs, and two anonymous reviewers made helpful comments on the

manuscript. I especially thank T. W. Arnold for his thorough and insightful revision of a previous draft.

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Wilson Bull., 107(2), 1995, pp. 388–396

ORNITHOLOGICAL LITERATURE

Eastern Birds. A Guide to Field Identification of North American Species. By James Coe. Color illustrations by the author. 1994. Golden Press, New York:160 pp. Softbound. $12.95.—Anyone who browses in the "Nature" section of a large general bookstore such as Barnes and Noble, Borders, or Walden is accustomed to finding new bird books upon each visit; not the ones for which we all receive countless fliers in the mail, but usually relatively inexpensive paperbacks in large or small format with titles like "Birds of America," "Birds you should know," "All about birds," and the like. They may be written by third-rate nature writers, or may even be pot-boilers by underpaid professional ornithologists. If illustrated with photographs, these are usually obtained from agencies, and they may include either misidentified species, taxidermic mounts, or both. If illustrated with artwork, the pictures are usually dreadful.

This has certainly been my experience, but recently I found a book that I had not yet, at that time, seen announced or advertised, and it was tucked inconspicuously among a host of other bird books, familiar and unfamiliar. I took a quick look through it and immediately decided to buy it and call it to the attention of *Wilson Bulletin* readers without waiting for a review copy.

For some reason, the name James Coe does not seem to be a "household word" among writers on American bird artists, but there is no question but that he belongs up there among the best. Golden Press does not appear to think of this book as a competitor to its earlier, long standard field guide, "Birds of North America," by Robbins, Bruun, and Zim (hereafter RBZ). Coe's book covers only "the eastern portion of North America, west to the foothills of the Rocky Mountains and south into Texas, skirting the eastern rim of the Edwards Plateau" (from the author's introduction). It is intended to be an "abridged guide" suitable for beginners. Coe tried to include enough species so that the beginner would be relatively unlikely to encounter birds not in his book, but leaving out rarities that most people will never see. As he himself realizes, anyone can quibble about his choices, but by and large I think he has done a good job. I do feel that the list price of $12.95 is unduly steep for a small softbound book, especially when the hardbound version of RBZ, with twice as many pages, currently lists for $15.00.

Although having many fewer species than the older guide, the text accounts for each species are often no longer. Measurements are given in the text rather than on the plates as in RBZ, and now include both inches and centimeters. The sonograms in RBZ elicited much debate as to their usefulness; they are omitted in Coe's book. The range maps are bolder and with less detail than in RBZ, and in spite of this being a book covering "the eastern portion of North America," the maps will be of little use to observers in much of Canada, as they extend only to the tip of Maine and southern Nova Scotia. In RBZ the maps extended, when appropriate, to the Canadian Arctic, Greenland, and even Iceland. Granted that most users of Coe's book won't be watching birds in the Arctic, still it should be of some interest to know where the migrants and wintering birds are coming from.

The introductory material strikes me as at least as thorough and as more readable than in RBZ. The diagrams naming the parts of a bird are less cluttered, as Coe has included a closeup of a Song Sparrow head to identify regions and markings in this area, as well as a Yellow-rumped Warbler for the names of the rest of the bird's parts; these occupy half a page. In RBZ this was done with a single painting of a Lark Sparrow occupying only one-third of a page, and hence much more densely lettered.

Coe's brief Appendix includes a two-page illustrated discussion of feeding birds, a paragraph on the advantages of joining "Birdwatchers' clubs and organizations," with a para-

graph each on the American Birding Association and the National Audubon Society, and a brief bibliography of magazines, books, and sound recordings; all of these, of course, could be expanded, and the ease with which such recommendations become obsolete is demonstrated by Coe's listing of the late lamented journal *American Birds.*

I have left until last a discussion of the illustrations, as these are what attracted me to the book in the first place and about which I am especially enthusiastic. They are by far the most consistently lifelike of any field guide illustrations of North American birds. Arthur Singer, the illustrator of RBZ, was a good friend, and I mean no disrespect when I say that he was *not* a truly great bird artist. Unlike most of today's bird painters, Arthur did not come from a boyhood bird-watching background—he was already a commercial artist when he first tried his hand at painting birds. RBZ has been sufficiently popular as to suggest that the Singer illustrations were adequate for identification, but one has only to compare the plates of, say, the spotted-breasted thrushes in the two Golden Press books to see what I mean by calling Coe's paintings "lifelike." They simply capture the personality of the individual species to a degree that Singer seldom attained.

This is not to say that I find all of Coe's paintings faultless. Like many other artists, Coe appears to believe that chickadees have itty-bitty bills (Singer's pointed chickadee bills are even worse, and his titmouse bills utterly wrong). This is a false impression, as can be attested to by any bander who has had occasion to extract an angry chickadee from a mist net. The length of the bills of Black-capped, Carolina, and Boreal chickadees is equal to the distance between the front of the eye and the base of the bill. Bills that are too short by this criterion are obvious in Coe's Black-capped Chickadees, but the error is masked in the Carolina and Boreal chickadees by the fact that he has painted the eyes too far forward in the head.

In general, I think Coe has been more successful with passerines than with non-passerines. The legs and feet of his Mallards, for example, are much too tiny. The figure of the Red-shouldered Hawk does not show the distinctively long legs of this species. With a little imagination, one can see the dusky-tipped primaries of the white immature Little Blue Heron, but this distinctive character is not mentioned in the text. Coe is in good company, however, as the *National Geographic* field guide appears to be the only work adequately figuring this, although Peterson mentions it and shows a Coe-like hint of it in his Western (but not Eastern) guide. A Ruffed Grouse in flight has stiff, cup-like wings for a fast getaway (as do so many galliform birds), and does not show the hawk-like spread primaries of Coe's figure. The red morph Eastern Screech-Owl looks like a stuffed toy. However, all of these comments are not meant to imply that Coe has not had some striking successes among non-passerines. His shorebirds are superior to those of Singer and to many of those of Peterson (compare, for example, their Upland Sandpipers). His Sandhill Crane and Great Blue Heron are also superior portraits, and he wisely abandoned taxonomic sequence to place these birds on the same plate; Great Blue Herons are widely known vernacularly as "cranes," and the direct comparison is obviously useful.

In spite of the individual flaws mentioned earlier, I still believe that, as a whole, Coe's portraits are the best to be found in any current North American field guide, and I look forward to his producing a companion volume on western birds for Golden Press.—Kenneth C. Parkes.

Evolutionary Differentiation in Morphology, Vocalizations, and Allozymes among Nomadic Sibling Species in the North American Red Crossbill (*Loxia curvirostra*) Complex. By Jeffrey G. Groth. Univ. California Publs. Zoology 127:xii+1–143, 34 figures, 14

tables. $17.00 (paperback).—The evolution and systematics of the Holarctic Red Crossbills (*Loxia curvirostra s.l.*) is one of the most enigmatic puzzles that face ornithologists. These crossbills are highly nomadic, wander widely, and breed in any place in any season, when conditions are suitable; yet they show considerable interpopulational variability, indicating that panmixia among morphs is not common. Jeffrey Groth (1) summarizes the natural history and taxonomy of the Red Crossbills, (2) quantifies patterns of morphological variation, (3) describes interpopulational variation in vocalizations, (4) determines the extent to which forms of crossbills identified by vocalizations also differ in body size, bill size, color, and allozymes, and (5) discusses the evolution and taxonomy of the group. This is an ambitious undertaking, but one that Groth handles well.

It has been obvious to ornithologists that there is a great deal of morphological variation in Red Crossbills. Nonetheless, dividing these birds into taxa has been especially difficult, particularly in North America, in part because of a paucity of breeding specimens. It was also recognized that there is variability in vocalizations, but few specimens were of known vocal type. For the present study, Groth assembled 720 individuals, with recorded vocalizations available for 616 (additional calls recorded by others were used in some analyses), and tissues for electrophoretic studies were saved from 561 (and 16 White-winged Crossbills, *L. leucoptera*). Using these birds, Groth has examined the relationships among vocal types, size, color, and allozymes.

Groth found that Red Crossbills could be divided into eight groups on the basis of their flight call (a '*chip*' call). Most of these groups have a wide geographic distribution. One each is found in the southern Appalachians and the Pacific Northwest and three others in both the northeast and the west. On the other hand, one call type was found from only one bird recorded in Newfoundland, and another was recorded only from birds in the Chiricahua Mts., in southeastern Arizona and may be a call type principally of Mexican crossbills. Groth found that size variation (nine measurements on fresh specimens and 21 on skeletons) within vocal groups was not great, but that the different vocal groups differed substantially and in many cases significantly among themselves. In general, the largest birds with the largest bills were found in the southwest (these were the only birds that could successfully extract seeds from robust cones) and the smallest in the northwest, northeast, and Appalachian Mountains (there was not enough material to include the Newfoundland sample in these analyses). In short, the different vocal groups are differentiated morphologically; the groups overlap to some extent, but variability in groups is not great; and intermediate individuals do not have intermediate vocalizations. What we cannot tell from these analyses, however, is if there might be ways other than vocalizations in which the Red Crossbills could be equally well divided. Although Red Crossbills are variable in coloration, there is little evidence that this variation is related to variation in vocalization.

The electrophoretic assessment of 30 protein systems (43 presumptive genetic loci) revealed little differentiation among the song types or between *L. curvirostra* and *L. leucoptera,* perhaps indicating very recent divergence. One can imagine that the variabity in the sizes of cones available would exert strong selection on bill morphology. Minor variations in call notes could have been stochastically established in local populations of crossbills, and these may have become effective species recognition cues, facilitating rapid speciation.

Groth recommends that eight sibling species be recognized. On a practical level, these will be difficult to identify, the principal differentiating feature—their calls—being behavioral, and at that not particularly useful for identification. As Groth notes (1993:51–52), "Despite differences on spectrograms, all flight calls, alarm calls, and excitement calls can be described by the term '*chip.*' Considerable practice may be necessary for human observers to learn these differences and use them reliably in the field." Needless to say, the identities of most of the type specimens for the many subspecies of Red Crossbills that have

been named are uncertain, so if usual conventions are followed, it will be difficult to determine what binominal names would be appropriate. Groth also emphasizes that individuals breeding in a particular place should not be considered to be a "population" as they may well comprise individuals from two or more of the sibling species.

All in all, this is a fine paper—lucidly written, well thought out, and clearly presented. I particularly applaud the inclusion of data—means, ranges, sample sizes, standard errors—in the appendices and the careful attention to collection sites and dates of collection. I think that it is unfortunate that more was not done with the tissues and that a method better suited to differentiating little-different taxa than gel electrophoresis was used, but we can anticipate that this will be done in the future. This paper will be widely cited, both in textbooks and in the primary literature. Groth and his editors are to be commended for a job well done.—J. D. Rising.

Birds of Massachusetts. By Richard R. Veit and Wayne R. Petersen, illus. by Barry W. Van Dusen. Massachusetts Audubon Society, Lincoln, Massachusetts. 1993. 514 pp. 24 illustrations, 133 maps of breeding species distribution, front and endpaper maps of Massachusetts. $39.95.—Veit and Petersen's "Birds of Massachusetts" is the latest milestone in Massachusetts' traditional leadership in American ornithology. A well-written, readable, and carefully documented work, this book is the most comprehensive book on the birds of this state since Edward Howe Forbush's giant classic 70 years ago. Appropriately, the forward is by Roger Tory Peterson, who calls it "an important addition to the ornithological literature and a model for other states to follow."

The bulk of the text is a meticulous status review of each of the 460 species recorded for the state; but the book contains far more information than even that ornithological feat. To briefly describe the chapters: "Regional Descriptions of Massachusetts" defines the eight chief physiographic or bio-regions of the state: Berkshire County, the Connecticut River valley, Worcester County, Essex County, the Sudbury River valley, the greater Boston area, southeastern Massachusetts, and Cape Cod and the Islands. "Aspects of Massachusetts Bird Life" includes sections on pelagic birds, colonial waterbirds, migration, and vagrancy. "Sources of Data" gives an exhaustive and specific list of the sources used and the criteria for acceptance of the data.

The species accounts are the principal content of the book, and provide a complete summary of the status and occurrence of all the 460 bird species confirmed to have occurred in Massachusetts through 1991. These include 196 regularly breeding species, 10 rare species, and 5 introduced species. Confirmed escapees from captivity have been wisely omitted. Species accounts begin with a concise overview of the world wide and North American distribution and breeding range, and include, as appropriate, breeding status, seasonal abundance, habitat preference, locality information, early and late seasonal dates, and maximum numbers. Species accounts are precisely and intelligently written. Maps for the breeding species include the information on Possible, Probable, and Confirmed Breeding collected during Massachusetts' pioneering Breeding Bird Atlas Project.

Anyone who has compiled state records will particularly appreciate the quality of this book. It is an essential handbook for all New England birders, an important state book, an admirable model, and an important addition to any birder's library.—Sally Laughlin.

THE VULTURES OF AFRICA. By Peter Mundy, Duncan Butchart, John Ledger, and Steven Piper, illus. by Duncan Butchart. Academic Press, Harcourt Brace Jovanovich, Publishers, New York. 1992:460 pp., 111 color plates with caption figs., 24 range maps, 11 geophysical maps, 30 numbered text figs., 33 black-and-white illustrations with caption figs., 47 tables, 123 pencil sketches. $118.50.—For some of us, vultures are endlessly fascinating creatures. Perhaps the intrigue begins as morbid curiosity sparked by images of throngs of huge birds that jockey for position at and even *inside* carcasses of large mammals on the African plain, or by the legendary patience of the vulture that sits hunched, eyeing with dispassion the death of a meal-to-be, becoming more animated, salivating even, as meal time draws near. These images are probably realistic, at least for some of the species some of the time. What Mundy, Butchart, Ledger, and Piper have accomplished here is to destroy these caricatures as they reveal the intricacies of the vultures' adaptations for a predominantly scavenging lifestyle and then document the ecological and behavioral diversity that exists among the vultures of Africa. However, vignettes found throughout the book remind us how vultures got their reputations. Examples include brief and humorous quotations describing Egyptian vultures as being "sick with repletion" and "clogged with gore." African vultures comprise 11 species, ranging in size from the small Hooded (*Necrosyrtes monachus*; 1.7 kg), Palm-nut (*Gypohierax angolensis*; 1.75 kg) and Egyptian (*Neophron percnopterus*; 2 kg) vultures to the enormous Lappett-faced (*Torgos tracheliotos*; 6.8 kg), Eurasian Griffon (*Gyps fulvus*; 7.4 kg), Cape Vulture (*G. coprotheres*; 9.4 kg), and Cinereous vultures (*Aegypius monachus*; up to 12.5 kg!).

This is a splendid, encyclopedic volume. Most of its many large-format pages are devoted to scrupulous species accounts which are lavishly illustrated by Duncan Butchart's many wonderful pencil sketches as well as by his formal color illustrations. For each species, the authors summarize historical and current information on distribution and abundance, field identification of all age classes, morphological and physiological specializations, feeding, mating, and nesting biology—in short, everything known about the birds. These chapters embody everything that is attractive about Bent's volumes and, like that work, contain enormous amounts of real information while managing to convey a sense of the awesome task humans face when they try to interpret nature.

Four excellent introductory chapters progressively narrow our focus to the details of individual species. The first chapter contains a global survey of vultures and what is known of their phylogeny and systematics, including arguments centering on the problematic placement of the New World vultures. These authors agree that the New World Cathartid vultures are probably modified storks, while the Old World Accipitrid vultures are related to hawks and eagles. Chapter 2 then focuses on the general characteristics that distinguish vultures from other birds, including exceptionally fine information on flight mechanics of long-distance soaring. It is slightly frustrating that the remarkable convergence between the Old World and New World vultures for their primarily scavenging lifestyles is not more fully developed. The authors can be forgiven, however, for this is a book about the African vultures, after all. When they peel their way down to that topic, beginning in Chapter 3 with discussion of Africa as a setting for vultures, there seemingly is no detail omitted. While the global comparisons make an interesting illustration of convergent evolution in action, it becomes obvious that Africa is vulture heaven; only on that continent and in a small area in India can one find as many as six different species at one carcass.

Following the species accounts are five chapters. The first of these compares in great detail the foraging, feeding, and social behavior of African vultures, and the second takes a comparative look at their breeding biology. This is precisely the stuff that first hooked me, almost 20 years ago, on vultures in general. How can these great animals rely on herds of ungulates that migrate over enormous distances and at the same time feed hungry off-

spring in a nest that is stationary? The answer is that most species do not rely on these herds, but those that do spend a lot of time flying great distances. Presumably constrained by this sporadic and unpredictable feeding regime, vultures are monogamous, lay small clutches (1 or 2 eggs) and their young grow slowly. Whether pairs nest in great aggregations or in isolation varies among species. Some species nest as solitary pairs and often feed in pairs or as the only member of their species, while others, like the griffons, seem to do everything in hordes, from their congregations at carcasses to their huge breeding colonies. These chapters are a treasure trove for behavioral ecologists. The variety of physiological, morphological, and behavioral mechanisms by which closely related species solve problems presented to them by their environments are well illustrated by the guild of African scavenging birds.

The final three chapters trace the history of the important relationship between humans and vultures on the African continent, the problems faced by vultures in modern Africa, and the efforts of the Vulture Study Group to protect these birds. The history is wonderful reading as we learn about the status of vultures as gods to the ancient Egyptians, as central figures through time as depicted in San art, and as food for 20th century Fernando Po and Ivory Coast (although in general vultures are rarely eaten, as "vulture flesh is an acquired taste, rather like roasted African termite alates, Greek olives, or American beer"). Many modern indigenous Africans use vulture body parts in folk medicines for their presumed clairvoyant properties (the superb vision and fast flight of vultures allow them to gather so quickly at carcasses that it seems that they foresaw the death). Finally, the authors devote a chapter essentially to themselves as charter members of the Vulture Study Group, an organization of activists committed to vulture conservation in Africa. The members include thoroughly modern scientists who study the effects of environmental poisons on vultures, document their interactions with modern technology such as high voltage power lines, and design and implement renovations to prevent wholesale electrocutions of vultures. They have established successful "vulture restaurants" that provide supplementary food for vultures in places in which food is thought to be limiting. These stations also allow detailed and up-close study of feeding interactions. The work of this group illustrates that people can, when armed with sufficient good information on the biology of declining populations, begin to address the problems those populations face in today's world.

This is a wonderful book about a group of birds that are so intriguing that they are prominent in folklore, even in distant cultures. The vultures of Africa are demystified by this exposure through good science, natural history, and art by a team of authors dedicated to their conservation.—Patricia G. Parker.

Animal Behavior. Edited by Tim Halliday, illus. by Barbara Rodanska and Jan Smith. Univ. of Oklahoma Press, Norman, Oklahoma. 1994. 144 pages, 251 color plates, 22 illustrations. $25.95.—This abundantly illustrated volume attempts to cover the breadth of animal behavior, with chapters on topics such as courtship, parental care, hunting, communication, anti-predator behavior, dominance hierarchies, symbioses, and adaptation to man. Each chapter is written by a separate author or pair of authors, mainly British or British-trained. Although the book deals with all animals, birds are given the prominence typically accorded to them in treatments of animal behavior, reflecting the importance of birds as subjects of study in ethology and behavioral ecology.

Overall, the book succeeds in conveying many of the central ideas and discoveries of the modern science of animal behavior in a format that ought to be attractive to the general public. Much emphasis is given to evolutionary costs and benefits of various behaviors,

with predominance given appropriately to the effects of the behaviors on the survival and reproduction of the individuals that perform them. Complex behaviors, such as honeybee dance language or communication in fireflies, are described and interpreted, albeit in simplified form. Complex theories are also presented, again in simplified but recognizable form, such as Triver's parental investment explanation for why female choice of mates is more prevalent than male choice. A great many interesting examples of peculiar behaviors are given, but always to illustrate some general theme, rather than simply to startle the reader with the strange and bizarre.

Illustrations are indeed abundant. On average, about half of each page is devoted to photographs and drawings and half to text, and no page is without illustration. The color photographs (obtained from a variety of sources) are particularly fine. One of the strengths of the book is the tight linkage that obtains between text and illustrations. If cleaning symbioses between mammals and birds are discussed in the text, then an illustration of such a symbiosis appears on the same or facing page; if a photograph shows a pair of electric fish, then the accompanying text discusses some aspect of electric fish behavior. Another strength of the book is the uniformity of style that has been achieved despite the diversity of the authors. All the chapters are written in the same relaxed and clear fashion with the same approximate mix of ideas and examples. This uniformity must be the product of some forceful editing.

The book does have some minor problems. For one, there are a few factual lapses. As one example, Charlotte Hosie, the author of a chapter on "Courting Rituals", states that in the 10% of bird species that are non-monogamous, males and females do not associate beyond copulation and that males do not participate in parental care. This statement overlooks the fact that many non-monogamous species of birds are polygynous or polyandrous rather than promiscuous and do have extended pair bonds and paternal care. Ornithologists will be surprised by a mention elsewhere in the text of the North American "rufous throated hummingbird"; sadly, this turns out from the accompanying photograph not to be a hitherto unknown hybrid but merely a mislabelled reference to the Rufous Hummingbird (*Selasphorus rufus*). A second minor problem is that the use of a largely British team of authors skews the examples away from those animals that would be more familiar to an American audience. Thus, urban scavengers are illustrated with hedgehogs (*Erinaceus europaeus*) rather than raccoons (*Procyon lotor*), and Great Tits (*Parus major*) and Greenfinches (*Carduelis chloris*) are used as examples of status signalling rather than Harris' Sparrows (*Zonotrichia querula*) and Dark-eyed Juncos (*Junco hyemalis*).

These problems are indeed minor and do little to detract from the overall value of the book, which provides a first rate means of introducing a general audience to the subject of animal behavior. Halliday and colleagues are to be commended for producing a volume that conveys so much of the science of behavior in such an attractive and engaging fashion.—William A. Searcy.

Dean of The Birdwatchers. A biography of Ludlow Griscom. By William E. Davis, Jr. Smithsonian Institution Press, Washington. 1994:xvi + 234 pp., 27 black-and-white photos. $29.95.—Ludlow Griscom was a complex and often controversial individual who strode across both the ornithological and birding worlds in the first half of this century. In some quarters, he is hailed as the founder of modern birding, and the one man who originated and developed the skills of bird identification in the field without the use of a shotgun. The title of this book reflects that view.

We have before us a scholarly biography by William Davis, who had access to the vo-

luminous Griscom correspondence, as well as the cooperation of the Griscom family. Over several years, he conducted interviews with many of Griscom's acquaintances. Much of the book consists of direct quotations from Griscom's letters and these give us an insight into his thought processes and personality. Davis has made an attempt to give us a balanced view of the good and the not-so-good of the man Griscom. He is fairly successful in this but as with most biographies the not-so-good is slighted. We do not really get a full view of the man's often abrasive personality, and the arrogance that is evident in some of his writings that are not quoted in the book.

Davis has wisely rejected the strict chronological order of describing Griscom's life and his varied activities. Part 1, "The Early Years," tells us of his background, education, and private life. Part 5, "The Final Years," describes the last decade of his life, when he was greatly handicapped by health problems. The intervening three parts are titled "Ornithology," "In the Field," and "Conservation."

The Ornithology Part treats his work at A.M.N.H. and M.C.Z. as well as his activities in the A.O.U. and the Nuttall Ornithological Club, and his association with the Boston Museum of Science. While there is a chapter on his ornithological expeditions, we really learn very little about these trips and his subsequent contributions to scientific ornithology. This is partly because while Griscom kept detailed bird lists for his expeditions he did not report detailed accounts of the expeditions. In fact, other than being told how many taxa he described, most of which turn out to be weakly differentiated subspecies, the reader gets little impression of his contributions to scientific ornithology. Although we are told that there were "anti-Griscom" factions among professional ornithologists, and indeed among the members of the Nuttall Club, the reasons for this are not clear.

The Conservation section details his work as Chairman of the Board of the National Audubon Society and his activity with the Massachusetts Audubon Society. This phase of his life and his extensive contributions to the conservation movement have not been adequately addressed in previous accounts of his activities.

But it is as the super-birder and field identification virtuoso that Griscom is best known today. The three chapters of Part three, "In The Field," are devoted to this topic. In one long chapter many people describe their experiences in the field with Ludlow on his strenuous birding days. These must have been a lot of fun. From these descriptions, one gets the impression that Griscom's enthusiasm for birds and birding made him a rather different person when birding in the field and that the darker facets of his personality were suppressed. It is apparent, though, that only a select few were invited on these outings.

The other two chapters belabor the points that Griscom is the man who invented the field identification techniques of birding, proved that birds need not be collected to identify them, and invented the sport of birding. The dust jacket identifies him as the "first birder" and one dust jacket blurb claims that he ". . . almost single-handedly turned birding with field glasses into a respectable pastime." This is myth. Myth formulated by the myopic view from behind the Boston-New York axis which does not admit that any birding in the modern sense took place west of the Hudson River during the critical years. In many places away from the northeast there were enthusiastic and highly skilled birders who had never heard of Ludlow Griscom. They too had abandoned the use of the collecting gun, and some of them had field skills approaching his. They were also engaging in the birding sport. Griscom's direct influence on most of the birders of the country was minimal. His real contribution was that he was the inspiration which led Roger Peterson to write his field guides. These made the task of learning how to identify birds easier, and so have had a real effect on the birding community. In fairness it should be said that Davis makes no such extravagant claims for Griscom, but makes it clear that his influence was mainly local.

The chapter on sight records and collecting points out that Griscom was caught in a

dilemma about collecting. His own skills had been developed by intensive study of museum collections, and he was adamant about having specimen records for rarities. The book closes with a complete bibliography of Griscom's writings, and by examining this, we do get some idea of his contributions to scientific ornithology.

Davis has worked on this book for several years and has succeeded in turning out an interesting account of the life of an interesting ornithologist. The book also gives us some insight into the ornithological world in the second quarter of this century. It fills a definite niche in ornithological historiography.—George A. Hall.

EDITOR'S NOTE

The above reviews are the last edited by George A. Hall as he will no longer be book editor after this issue. His duties are being taken over by William E. Davis, Jr. (see inside back cover for new address for book review editor).

George Hall has served The Wilson Ornithological Society for many years, first as editor of the journal for ten years, and later as review editor for another 10 years. All who have worked with George during his tenure will agree about his fair, impartial, and kind treatment of manuscripts and their authors. George has helped many young ornithologists with their first research papers. He edited one of my first published studies—a note on nighthawks—and I will not forget (and will always try to emulate) his considerate manner. Many thanks, George, for your long, patient, skillful service.—C. R. Blem.

This issue of *The Wilson Bulletin* was published on 2 June 1995.

The Wilson Bulletin

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CONTENTS

MAJOR PAPERS

HISTORIC AND TAXONOMIC IMPLICATIONS OF RECENTLY FOUND ARTWORK IN ARITHMETIC BOOKS OF STUDENTS OF ALEXANDER WILSON ..... *Edward H. Burtt, Jr. and William E. Davis, Jr.* 193

PHYLOGENY AND COMPARATIVE ECOLOGY OF STIFF-TAILED DUCKS (ANATIDAE: OXYURINI) ..... *Bradley C. Livezey* 214

MORPHOLOGICAL AND GENETIC DIVERGENCE AMONG ALASKAN POPULATIONS OF *BRACHYRAMPHUS* MURRELETS ..... *Jay Pitocchelli, John Piatt, and Matthew A. Cronin* 235

SHEEP CARCASS AVAILABILITY AND USE BY BALD EAGLES ..... *N. Vern Marr, W. Daniel Edge, Robert G. Anthony, and Ray Valburg* 251

FOOD HABITS OF BALD EAGLES BREEDING IN THE ARIZONA DESERT ..... *Teryl G. Grubb* 258

BREEDING BIOLOGY OF SNOWY PLOVERS AT GREAT SALT LAKE, UTAH ..... *Peter W. C. Paton* 275

EASTERN BLUEBIRDS ARE ATTRACTED TO TWO-BOX SITES ..... *Jonathan H. Plissner and Patricia Adair Gowaty* 289

PLASMA CORTICOSTERONE LEVELS IN TWO SPECIES OF *ZONOTRICHIA* SPARROWS UNDER CAPTIVE AND FREE-LIVING CONDITIONS ..... *Peter P. Marra, Kevin T. Lampe, and Bruce L. Tedford* 296

SOME FACTORS AFFECTING PRECISION OF THE TOTAL BODY ELECTRICAL CONDUCTIVITY TECHNIQUE FOR MEASURING BODY COMPOSITION IN LIVE BIRDS ..... *Andreas Asch and Daniel D. Roby* 306

AVIAN PREDATION AT PENGUIN COLONIES ON KING GEORGE ISLAND, ANTARCTICA ..... *Steven D. Emslie, Nina Karnovsky, and Wayne Trivelpiece* 317

HATCHING, GROWTH, AND MORTALITY OF MAGNIFICENT FRIGATEBIRD CHICKS IN SOUTHERN BAJA CALIFORNIA ..... *Roberto Carmona, Juan Guzmán, and Juan F. Elorduy* 328

INTENSITY AND CHRONOLOGY OF POSTREPRODUCTIVE MOLTS IN MALE CANVASBACKS ..... *Jonathan E. Thompson and Ronald D. Drobney* 338

SHORT COMMUNICATIONS

MOLT CHRONOLOGY OF MALE MALLARDS WINTERING IN MISSOURI ..... *Daniel L. Combs and Leigh H. Fredrickson* 359

HABITAT USE BY WINTERING AND BREEDING BIRD COMMUNITIES IN RELATION TO EDGE IN AN IRRIGATED FOREST ..... *Richard H. Yahner* 365

SEQUENCE OF PLUMAGE EVOLUTION IN THE STANDARDWING BIRD OF PARADISE ..... *Gary R. Graves* 371

ROOSTING BEHAVIOR OF PROTHONOTARY WARBLERS IN THE NON-BREEDING SEASON ..... *Ian G. Warkentin and Eugene S. Morton* 374

TIME OF DAY OF EGG LAYING BY EASTERN BLUEBIRDS ..... *Susan B. Meek and Raleigh J. Robertson* 377

SEX-BIASED KLEPTOPARASITISM OF HOODED MERGANSERS BY RING-BILLED GULLS ..... *Felipe Chavez-Ramirez* 379

INTRASPECIFIC VARIATION IN EGG COMPOSITION ..... *Wendy L. Hill* 382

ORNITHOLOGICAL LITERATURE 388

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 107, NO. 3 SEPTEMBER 1995 PAGES 397–576

(ISSN 0043-5643)

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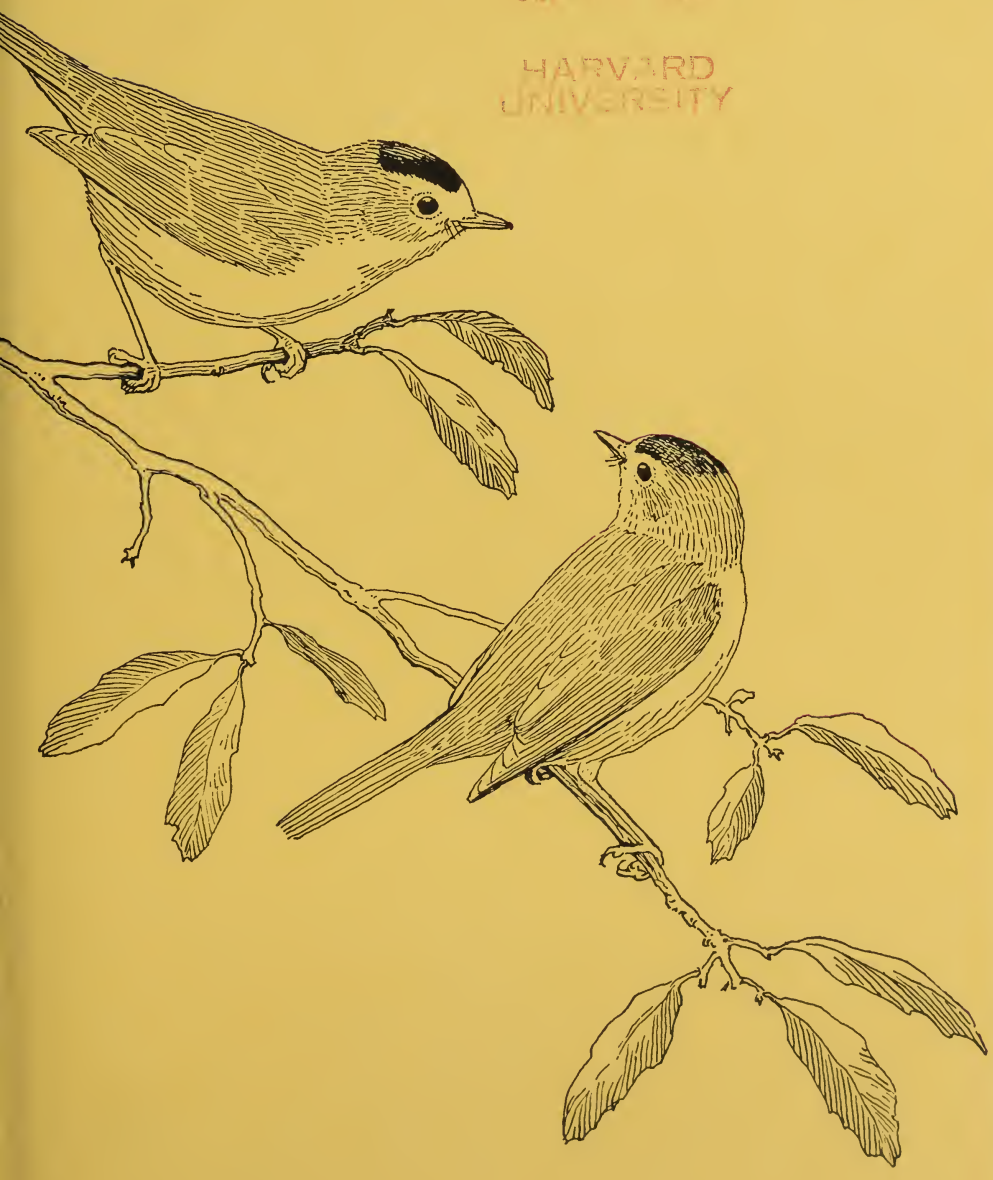

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THE WILSON BULLETIN
(ISSN 0043-5643)

THE WILSON BULLETIN (ISSN 0043-5643) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Second-class postage paid at Lawrence, KS. POSTMASTER: Send address changes to THE WILSON BULLETIN, P.O. Box 1897, Lawrence, KS 66044-8897.

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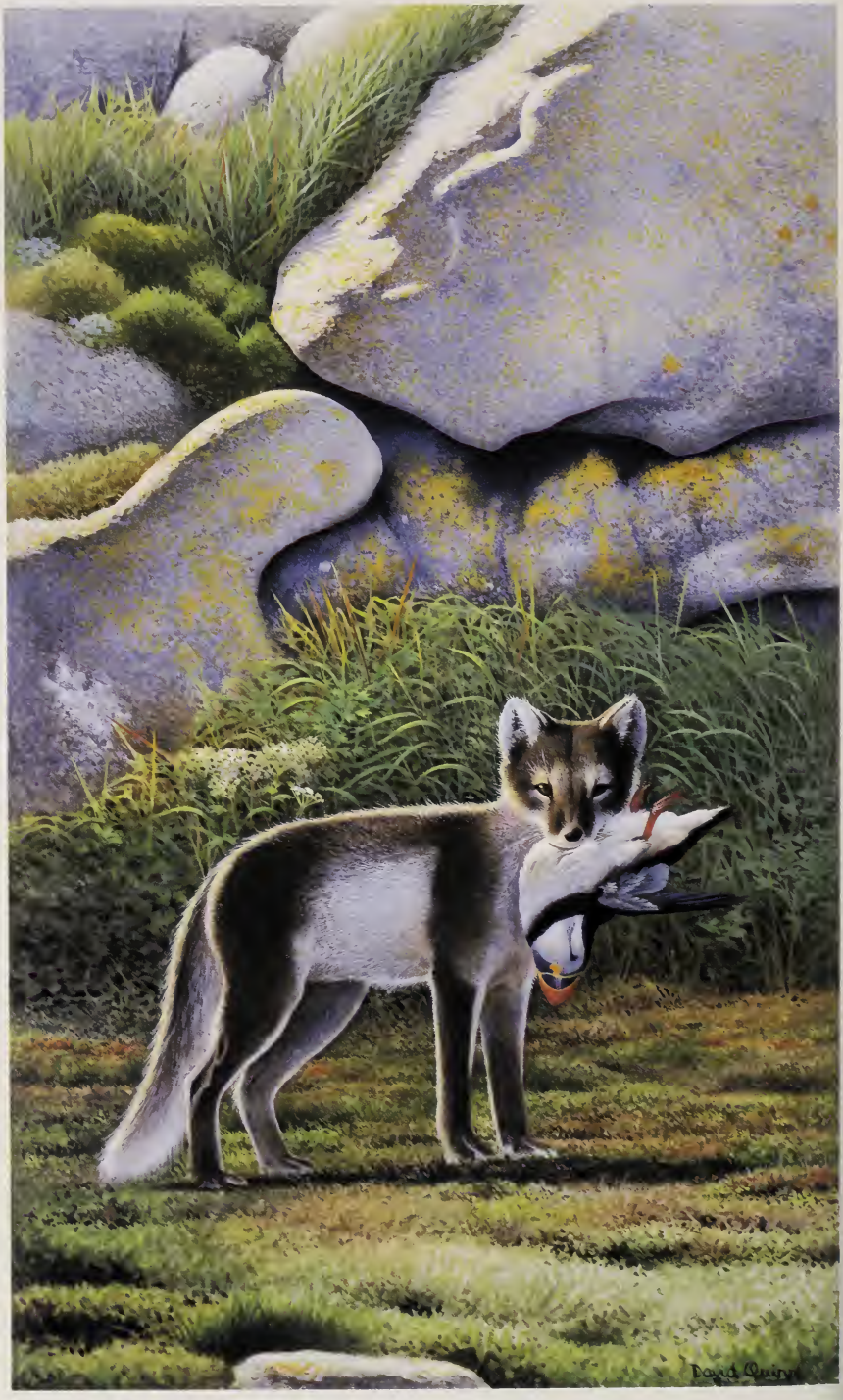

Arctic fox *Alopex lagopus* with Atlantic Puffin *Fratercula arctica* at the Gannet Islands, Labrador, 1992. Painting by David Quinn. [Editor's note: this painting has recently been stolen, and T. R. Birkhead would appreciate any information concerning its whereabouts.]

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 107, NO. 3 SEPTEMBER 1995 PAGES 397–576

Wilson Bull., 107(3), 1995, pp. 397–412

ARCTIC FOX INFLUENCE ON A SEABIRD COMMUNITY IN LABRADOR: A NATURAL EXPERIMENT

T. R. BIRKHEAD[1] AND D. N. NETTLESHIP[2]

ABSTRACT.—The Gannet Islands contain the single most important seabird colony in Labrador, both in terms of numbers and species diversity. In 1992, we discovered arctic foxes (*Alopex lagopus*) on these islands during the breeding season. Of five islands examined, two had resident foxes (in one case breeding), two had been visited by foxes earlier in the season, and one had no foxes and had not been visited. A comparison of these islands in 1992 and with our detailed studies from the early 1980s, revealed the effect that foxes had had on seabirds. On islands with foxes, Razorbills (*Alca torda*), Common Murres (*Uria aalge*), and Thick-billed Murres (*U. lomvia*) had ceased breeding. Atlantic Puffins (*Fratercula arctica*) continued to attempt to breed, but fox predation on adult birds and eggs was intense and breeding success low. On islands visited by foxes earlier in the season, the number of breeding Razorbills was reduced, and breeding by Common Murres was delayed by 2–3 weeks. *Received 12 Dec. 1993, accepted 1 Nov. 1994.*

The selection of breeding areas by birds is determined mainly by the proximity of feeding areas and safety from predators (Lack 1968). There is good circumstantial evidence that marine birds breed on offshore islands and on steep mainland cliffs to avoid terrestrial predators (Larson 1960, Lack 1968). Where predators have been introduced to islands by man, ground-nesting seabirds have usually been rapidly extirpated (Moors and Atkinson 1984, Burger and Gochfeld 1994). For example, between 1750 and the 1930s arctic foxes (*Alopex lagopus*) and red foxes (*Vulpes vulpes*) were introduced to about 450 Alaskan islands for fox farming: their effect on the ground-nesting birds was disastrous (Sekora et al. 1979, Bailey 1993, Bailey and Kaiser 1993). In other areas where foxes and

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seabirds coexist, it is clear that the foxes have been a major factor influencing the habitat selection of the birds (Fisher and Lockley 1954, Larson 1960, Petersen 1982, Bailey 1993).

Although the end result of introducing foxes onto seabird islands is well known, the actual process by which it occurs has not previously been described. In the present paper, we describe the consequences of a natural invasion of arctic foxes onto a seabird colony in Labrador. Our study was unique in that the seabird colony at the Gannet Islands, Labrador, comprises several adjacent islands (Fig. 1), some of which held foxes and some which did not during our study. We thus had a 'natural experiment' in which we could determine which effects were the results of foxes and which were due to other causes.

STUDY AREA AND METHODS

The Gannet Islands (53°56′N, 56°32′W) constitute the largest and most diverse seabird colony in Labrador (Nettleship 1980, Nettleship and Glenn 1992). In 1983, when the most detailed census was conducted, the breeding seabird community at the Gannet Islands comprised the following: 13 pairs of Northern Fulmars (*Fulmarus glacialis*), about 14 pairs of Leach's Storm-Petrel (*Oceanodroma leucorhoa*), 100 pairs of Great Black-backed Gulls (*Larus marinus*), 52 pairs of Black-legged Kittiwakes (*Rissa tridactyla*), 4930 pairs of Razorbills (*Alca torda*), 38,350 pairs of Common Murres (*Uria aalge*), 965 pairs of Thick-billed Murres (*U. lomvia*), 35 pairs of Black Guillemots (*Cepphus grylle*), and 41,300 pairs of Atlantic Puffins (*Fratercula arctica*) (Nettleship et al. 1984, Birkhead and Nettleship 1987a). Northern Fulmars, Great Black-backed Gulls, and most Common Murres and Razorbills bred in open habitat relatively accessible to terrestrial predators. Leach's Storm-Petrels and Atlantic Puffins nested in earth burrows, and Black Guillemots nested in rock crevices under boulders. Only Black-legged Kittiwakes and Thick-billed Murres bred on cliff ledges. Prior to the present study, we had conducted detailed investigations of the reproductive ecology of the seabirds, particularly the alcids, at this colony between 1981 and 1983 (Birkhead and Nettleship 1983, 1987a,b,c, 1988; Birkhead et al. 1985a,b; D. N. Nettleship, unpubl. data).

The Gannet Islands comprise a total of seven small islands: a group of five adjacent islands (referred to as the Gannet Clusters and identified as GC1 through GC5 which lie within 500 m of each other, see Fig. 1), Western Gannet (also referred to as GC6) which lies 1.5 km to the west of GC1, and Outer Gannet which lies 7 km north of the Gannet Clusters (Fig. 1). The islands vary in area from 4.4 ha (GC4) to 125 ha (GC6). All are low-lying (maximum height: 66 m above sea level) and are mainly rocky with heath scrub vegetation. The nearest point on the mainland is at Grady, about 17 km away.

In general, the summer (July–August) climate along the Labrador coast is cool: mean daily temperatures are about 10°C. Between December and late May, the sea ice is extensive and continuous from beyond the Gannet Islands to the adjacent mainland and to the north (Birkhead and Nettleship 1987a). The observations recorded here were made in July and August 1992 during which time temperatures on the Labrador coast were particularly low (Atmospheric Environmental Service, Environment Canada, Cartwright), possibly associated with the eruption of Mount Pinatuba in the Phillipines which is thought to have caused a global decline in temperatures through an increase in aerosols (Kerr 1993).

The present study was made on the Gannet Clusters (GC1 through to GC5) between 30

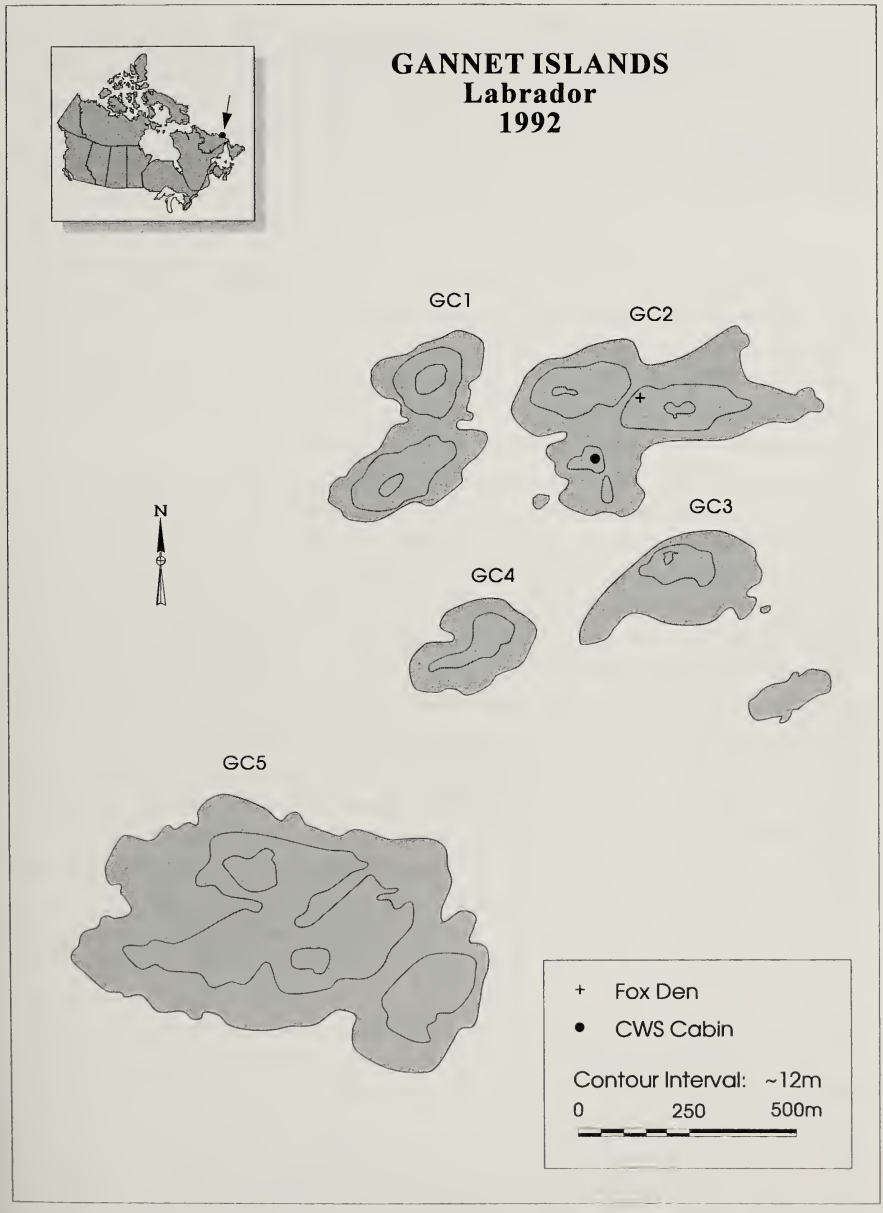

FIG. 1. Sketch map of five of the seven islands comprising the Gannet Islands (GC1 to GC5), Labrador, showing the approximate locations of the arctic fox den found on GC2 in 1992 and the main CWS research cabin. Inset map shows general location of the Gannet Islands archipelago in eastern Canada.

July and 13 August 1992. Previously, during the early to mid 1980s, we had documented the timing of breeding and breeding success of seabirds at the Gannet Clusters using standardized techniques (Nettleship 1976; Birkhead and Nettleship 1980; Birkhead and Nettleship 1987a,b,c). During the present study, we collected information that allowed us to make comparisons with information obtained in the 1980s and to determine the effect of arctic foxes on breeding performance of the seabirds. We also compared the breeding biology of seabirds in 1992 on those islands with and without foxes.

RESULTS

In 1992, there were resident foxes on GC2: a breeding pair and their two 8–10 week-old offspring. On GC5 there were two adult foxes, but we found no evidence of breeding. At the time of our visit, there were no foxes on GC1, GC3 or GC4, but we obtained clear evidence that foxes had been on GC4, circumstantial evidence that foxes had been on GC3, and no evidence whatsoever that foxes had been on GC1.

Prior to our observations in 1992, there were no records of arctic foxes spending the summer months on any of the Gannet Islands, even though the islands have been examined from the 1920–1930s (Austin 1932, Todd 1963) and 1950s (Tuck 1953, 1961), through the 1970s (1972, 1978, 1979) to the mid 1980s (Nettleship 1980, 1981; Birkhead and Nettleship 1983; Nettleship and Evans 1985; Birkhead and Nettleship 1987a,b,c). According to local people, arctic foxes occur regularly on the adjacent mainland during the winter months (Brice-Bennett 1977; see also Banfield 1974, Nowak 1991), but all observers (including Cartwright 1792, Townsend 1911, Harper 1960, Brice-Bennett 1977) also point out that arctic foxes usually disappear (in a northerly direction) again in the spring. It seems likely that arctic foxes move south in Labrador during the winter, sometimes traveling over the sea ice, and in this way reached the Gannet Clusters. We do not know when the foxes we observed in 1992 first reached the Gannet Islands, but circumstantial evidence suggests that it might have been several winters prior to the 1991–1992 season. There was an influx of arctic foxes onto the north shore of the Gulf of St. Lawrence during the winter of 1987–1988 (G. Chapdelaine, pers. comm., CWS-Quebec Region files), associated with particularly heavy ice. It is possible that the foxes we observed also arrived on the Gannet Islands during that winter (see below).

Our camp was on GC2 where we were able to observe the foxes directly. They spent much of their time in the Atlantic Puffin subcolony searching for eggs and adults. Although we saw them obtain eggs on numerous occasions, we did not witness foxes capturing or killing adult puffins (Frontispiece). We did, however, see foxes carrying recently killed puffins and found numerous freshly dead adult puffins and a fox cache comprising 26 Atlantic Puffins, three Common Murres, and two Razor-

bills. We also found two dead Razorbills, which we presumed to have been killed by foxes, under boulders in their breeding colonies.

Seabird Breeding Biology

There was no evidence of any recent or past presence of arctic foxes on GC1 in 1992, so we have used the biology of the seabirds on this island as our baseline against which to compare the other islands.

Common Murre.—We had no previously established study plots on GC1 so we were unable to make any quantitative comparisons of the proportion of sites occupied in 1992 compared with the 1980s. However, our subjective impression, and comparisons of photographs taken in the 1980s, indicated that there had been no reduction in the number of breeding Common Murres. On 3 August, we examined one group of breeding Common Murres considered typical of the GC1 murre population and found 106 chicks and 48 eggs; thus by this date 69% of eggs had hatched. We measured the wing length of 57 chicks and found the mean to be 33.82 mm ± 4.85 SD, and the longest wing length 44 mm. Comparison of standard growth curves obtained in the 1980s for Common Murre chicks at the Gannet Islands (T. R. Birkhead and D. N. Nettleship, unpubl. data) indicated that the chick with the longest wing length was 10 days old and had therefore hatched on 28 July. In the 1980s, the mean interval between first hatching and the median hatching date was 6 days (range: 4–9 d). Assuming that the first hatching date in 1992 was 28 July, the median hatching date was around 3 August 1992.

Thick-billed Murre.—Counts of Thick-billed Murres in 1992 showed that their numbers on GC1 (and elsewhere on the Gannet Clusters) had increased substantially since the 1980s (D. N. Nettleship and T. R. Birkhead, unpubl. data). Casual inspection of chicks on breeding ledges during feeding observations (without disturbing birds from ledges) revealed 19 eggs and 19 chicks on 8 August, which suggests that the median hatching date was around this time.

Razorbill.—In the 1980s, we established two Razorbill study plots on the northern end of GC1. On 3 August 1992, we examined one of these to determine the proportion of sites occupied by breeding birds and the proportion of eggs and chicks. (The other study plot was not examined in detail to avoid disturbing the large numbers of Common Murres breeding close by.) We found that all 110 Razorbill breeding sites identified in the 1980s were occupied and that there were an additional 11 occupied sites within the boundaries of the study plot. There were 93 eggs and 28 chicks: 23% chicks, most of which we estimated to be about 1–3 days old. We therefore assumed that the first chicks had hatched on 31 July. In the 1980s, the mean interval between first and median hatching dates

TABLE 1

TIMING OF BREEDING OF ALCIDS AT THE GANNET ISLANDS, LABRADOR, IN THE EARLY 1980S AND IN 1992[a]

Species	Median hatching 1981–1983	Median hatching 1992
Razorbill	23 July–4 August	9 August
Common Murre	16–26 July	3 August
Thick-billed Murre	22–28 July	3 August
Atlantic Puffin	30 July–10 August	14 August

[a] Values given are the range of median hatching dates for the 1980s and the estimated median hatching dates for birds undisturbed by arctic foxes on Island GC1 in 1992 (see text).

was nine days (D. N. Nettleship and T. R. Birkhead, unpubl. data), so we assumed that in 1992 the median hatching date for Razorbills on GC1 was 9 August.

Atlantic Puffin.—In the 1980s, the density and occupancy of Atlantic Puffin burrows were determined in 10 areas on GC1. In 1992, on 11 August, five of those areas were re-examined. We found 151 of 176 (89%) burrows to contain either an egg (N = 143) or a newly hatched chick (N = 8). All eight chicks were probably less than one day old (based on wing length), and four were still wet, indicating that they had only recently hatched. We therefore assumed that the first chicks hatched on 11 August in 1992. In our previous studies, we found that the mean interval between first and median hatching dates was three days (D. N. Nettleship and T. R. Birkhead, unpubl. data), so we estimated that the median hatching date in 1992 was 14 August.

Table 1 shows the estimated timing of breeding of four alcid species on GC1 in 1992 and compares these values with those obtained in the 1980s. It is clear from these comparisons that the timing of breeding in 1992 was considerably later than we had previously recorded. Razorbills and Common Murres were between one and two weeks later than in the 1980s, and Thick-billed Murres and Atlantic Puffins about one week later. Presumably the delay in breeding was associated with the relatively low summer temperatures in 1992.

The Effects of Arctic Foxes on Seabirds on Islands GC2 and GC5

Island GC2.—In 1992, a pair of arctic foxes and their two offspring were present on GC2. In the 1980s, we recorded 1219 pairs of breeding Razorbills in five subcolonies on this island, but in 1992 all Razorbill subcolonies were abandoned. The adult birds spent most of their time in rafts on the sea directly opposite their subcolony location. Occasionally

in the evening, Razorbills alighted on rocks adjacent to the subcolonies, but they were nervous and rarely stayed long. We found one whole Razorbill egg (apparently deserted) and the remains of 12 other egg shells at breeding sites in the subcolonies, indicating that some birds had attempted to reproduce in 1992. We also found Razorbill eggs (none of which showed signs of incubation) and dead adult Razorbills which had been cached by foxes. Judging from the vegetation in the Razorbill colonies, especially around the individual breeding sites, it was clear that many sites had not been used in either the 1992 season or in one or more seasons before that, which suggests that foxes might have been present on GC2 for several seasons.

Also on GC2 in 1983, we recorded 50 pairs of Common and 19 pairs of Thick-billed Murres, but in 1992 we found no murres breeding on GC2. There was no evidence that Common Murres were visiting their breeding colonies in 1992. However, the Thick-billed Murre breeding ledges had large amounts of conspicuous pink guano, typical of this species elsewhere on the Gannet Clusters, indicating that they had been regularly visited. Indeed, on a number of occasions adult Thick-billed Murres were seen on these ledges. The Common Murre breeding sites on GC2 were similar to those of the Razorbill, located in low-lying boulder areas and hence extremely accessible to foxes. The Thick-billed Murre breeding areas on GC2 were located on a steep cliff, but a deep crack running from the top of the island past the breeding ledge made the ledge readily accessible to humans and hence presumably foxes.

In the 1983 census of GC2, we had also recorded 13 breeding pairs of Northern Fulmars but found none in 1992. Indeed, we saw only a single adult fulmar, far offshore from the Gannet Islands, during our entire visit in 1992. In 1983, we recorded 12 pairs of Black Guillemots breeding on GC2, whereas none appeared to be breeding in 1992 although birds were seen regularly on the water (maximum count: 24 individuals).

In 1983, the breeding population of Atlantic Puffins on GC2 was estimated to be 6192 pairs (Nettleship et al. 1984). In 1992 on 9 August, a sample of 112 burrows was examined. Of these, 41 (36.6%) were empty and inactive and 71 (63.4% burrow occupancy) contained either nest material or an egg or shell fragments and were assumed to have been occupied during the 1992 season. Of the 71 active burrows, only 13 (18.3%) contained an egg. Comparable values for 1983 were 77.6% burrow occupancy (280 of 356 burrows), with 40% of these active burrows with an egg or chick. Differences between years for burrow occupancy and nest status were highly significant ($P < 0.001$), with rates lower in 1992 when foxes were present than in 1983 when they were not (occupancy: $\chi^2 = 10.58$, 1 df; nest status: $\chi^2 = 11.62$, 1 df).

Island GC5.—On GC5 where there were two resident adult arctic foxes the effect on the seabirds was similar to that on GC2. Where we had found 1213 pairs of Razorbills in 1983, we found just two breeding pairs in 1992. Both of these were incubating on small ledges on a steep cliff and were presumably inaccessible to the foxes. We also found one partly eaten adult Razorbill and remains of five Razorbill eggs, along with several hundred predated puffin and murre egg shells. Where there had been approximately 250 breeding pairs of Common Murres in 1983, there was none breeding in 1992. The estimated number of Atlantic Puffins breeding on GC5 in 1983 was 7,780 pairs. In 1992 a sample of 117 burrows was examined on five plots on 11–12 August, of which 60 (51.3%) were empty and had apparently not been used in the 1992 season and a further 57 (48.7%) were active and contained either nest material or an egg. Of the 57 active burrows 14 (24.6%) contained an egg; no eggs had hatched. Comparable figures for 1983 were 92.9% burrow occupancy (N = 365) with 234 of 339 active burrows (69%) with eggs or chicks. These inter-year differences for puffins were highly significant ($P < 0.001$) with burrow occupancy and sites with an egg or chick (nest status) much higher in 1983 than 1992 when foxes were present (occupancy: $\chi^2 = 117.86$, 1 df; nest status: $\chi^2 = 41.22$, 1 df).

The Effects of Arctic Foxes on Seabirds on Islands GC4 and GC3

Island GC4.—There were no foxes present on this island during our visit, but the presence of fox scats, cached Common Murre eggs (N = 6) and Atlantic Puffin eggs (N = 4), a cached adult puffin, and the corpses of adult puffins made it clear that foxes had been present earlier in the season.

In 1983, we established three Razorbill study plots (A, B, C) on GC4, and these were re-examined in 1992. Plot A, which had 45 active sites in 1983, contained just seven eggs and 13 empty sites on 4 August 1992. Plot B (43 sites in 1983) contained six eggs and 17 empty sites on 4 August 1992, and Plot C (25 sites in 1983) contained nine eggs and 16 empty sites between 4 and 13 August. Overall, we estimated that about 20% of the sites occupied by Razorbills in 1983 were being used in 1992. As with GC2 and GC5, our impression was that numbers of adult birds near the GC4 colonies were similar to those in the 1980s: only the number with eggs was reduced. No Razorbill chicks were observed at either Plots A or B on 4 August, and no chicks were seen at Plot C which was observed on most days up until 13 August. By comparison, on GC1 on 3 August we found 93 chicks and 28 eggs, a difference that is highly significant ($\chi^2 = 43.50$, 1 df, $P < 0.001$), indicating that the timing of egg-laying on GC4 was later than on GC1.

The number of Thick-billed Murres on GC4 in 1983 was 866 individuals, but in 1992 we recorded a total of 1585 birds. Elsewhere on the Gannet Clusters, Thick-billed Murre numbers had also increased (D. N. Nettleship and T. R. Birkhead, unpubl. data). The first Thick-billed Murre chick was observed on 1 August 1992. Our qualitative observations suggested that the timing of breeding of Thick-billed Murres on GC4 was similar to that on GC1.

In the 1980s, our most detailed observations were made on Common Murres breeding in two study plots on GC4: CM-A (250 pairs) and CM-B (70 pairs). In 1992, we made observations at CM-A only. However, detailed comparisons between the two time periods were hampered because shifting rocks had altered the configuration of breeding birds and prevented us from re-identifying certain sites. When observations began on 1 August 1992, most Common Murres on CM-A were incubating. Few new eggs were detected subsequently, and no Common Murre chicks had hatched by the time observations ceased on 13 August. Given that the mean incubation period for Common Murres is 33 days and that the mean interval between the first and median hatching dates during the 1980s was about six days (range: 3–8 d) (Birkhead and Nettleship 1987a), this suggests that the median hatching date in 1992 fell between 19 August (at the earliest) and 30 August (latest). The timing of breeding of Common Murres on GC4 was therefore 2–3 weeks later than those on GC1.

The status of breeding sites on CM-A was assessed without disturbing the birds (using Type I observation procedures: see Birkhead and Nettleship 1980). Although it was impossible to determine the precise status of every site, our observations showed that a maximum of 180 sites were occupied by incubating birds in 1992. In the 1980s, the mean hatching success of the 250 pairs on this plot was 85% (Birkhead and Nettleship 1987b), so if the number of breeding pairs had remained the same and hatching success in 1992 was similar to the 1980s, the minimum number of pairs incubating eggs would have been 212 (250×0.85) rather than 180. It is not possible, however, to determine with 100% certainty whether reduction was due to the change in configuration of the study plot or to some other cause such as foxes. However, although certain rocks had moved since 1983, the arrangement of birds in 1992 was not very different (based on careful examination of 1982–1983 study plot photos). That suggests that most of the reduction in the total number of active sites was probably caused by something other than alteration of rock positions.

No observations of Atlantic Puffins on GC4 were made in 1992. All

Black-legged Kittiwakes at the Gannet Islands bred on sea-cliffs on GC4 and GC1—there was no evidence that they had been affected by foxes.

Island GC3.—On GC3 we had no direct evidence for the presence of foxes earlier in the 1992 season, although there were strong circumstantial evidence for the localized effect of some sort of predator. In 1983, we established one Razorbill plot on GC3 with 56 sites: on 2 August 1992 we found 22 eggs (39.3%) and 34 empty sites at this plot. Just as with GC4, laying appeared to have occurred late compared with GC1 (see above). In an adjacent area, however, we found newly hatched Razorbill (and Common Murre) chicks, which we estimated to be 1 or 2 days old, indicating that timing of breeding by some birds was similar to those on GC1.

No Common Murre study plots were established on GC3 during the 1980s. In 1992, therefore, we examined one small group of Common Murres adjacent to the Razorbill study plot. This area contained 113 eggs and 24 (17.5%) chicks, all of which appeared to be one or two days old. We therefore assumed that the first chicks hatched on 31 July 1992. We measured the dimensions of 100 Common Murre eggs that were being incubated: the mean volume index (length $\times$ breadth^2) was 212.68 cm^3 $\pm$ 17.07 SD was smaller than comparable samples measured in the 1980s (the difference between 1992 and 1981 and 1982 was significant [$P < 0.001$], but that between 1992 and 1983 was not [$t = 1.23$, 348 df, $P > 0.05$]). The smaller egg size in 1992 is consistent with that year being a relatively later breeding season (see Table 1).

We also examined a Common Murre breeding area on the northwest side of the island which had been photographed in 1978 (see Birkhead and Nettleship 1980: Fig 6) and in 1983 was estimated to contain about 1000 pairs (Nettleship et al. 1984). In 1992, this area was found to contain 1800 abandoned eggs. Many of the eggs were broken from having rolled off their sites, some had been opened by predators (possibly Great Black-backed Gulls, which breed on all the Gannet Islands), and many were still intact. All eggs were cold, and none appeared to have been incubated. However, among the abandoned eggs was a single group of 10–15 adult Common Murres (on small gravel area between the boulders: lower mid photo, Fig. 6 in Birkhead and Nettleship 1980) with five recently hatched murre chicks which were each attended by one or two adults.

In order to estimate when the murre eggs might have been abandoned, we opened a sample (N = 6) of eggs and measured the total, unstraightened embryo length. The mean volume index of abandoned eggs (212.00 cm^3 $\pm$ 18.43 SD, N = 85) was very similar ($t = 0.26$, 183 df, NS) to that of the 'live' eggs measured on GC3 (see above). Embryos averaged about 2.5 cm in length, which we estimated to be approximately half way

(i.e., about 16 days) through the 33 day incubation period (see Mahoney 1979 and Mahoney and Threlfall 1981 for details of aging murre embryos). Assuming the median laying date to be 3 July (see above), the subcolony must have been abandoned somewhere around 19 July 1992. No Atlantic Puffin burrows were examined on GC3 nor were any Thick-billed Murre breeding sites.

DISCUSSION

The effect of resident arctic foxes on breeding seabirds on GC2 and GC5 was dramatic, mainly because of the accessible nature of the breeding sites on these islands. With the exception of most Thick-billed Murres which breed on narrow ledges on steep cliffs at the Gannet Islands (Birkhead and Nettleship 1987b), and were thus inaccessible to foxes, all other species had either abandoned breeding (Common Murres, Razorbills, and possibly Black Guillemots), or like Atlantic Puffins, had attempted to breed but had suffered a high rate of egg loss through a combination of predation by foxes or disturbance. Although we found that between 18 and 25% of active puffin burrows contained either an egg or chick, it seems likely that with continued predation by foxes on GC2 and GC5, few if any Atlantic Puffin chicks would fledge from GC2 or GC5 in 1992.

The situation on GC4, where only 20% of Razorbills appeared to be breeding, and Common Murres were breeding two or three weeks later than on GC1, is more difficult to interpret. The most likely situation is that one or more foxes were present there until the time that Common Murres and Atlantic Puffin first started to lay eggs, probably early July. The presence of a fox on the island may either have deterred some birds from breeding or birds may have laid but then abandoned their eggs. However, since there were no obvious signs of abandoned eggs (as on GC3), the former seems more likely. Once the fox had disappeared from GC4, either by swimming or via a piece of ice, or perhaps after its accidental death, some birds may have resumed breeding. The consequences of late breeding for both Common Murres and Razorbills are not known, but most available evidence suggests that breeding success and the survival of late fledging chicks would be reduced (Nettleship 1972, Birkhead and Harris 1985, Harris 1992).

On GC3, localized abandonment of the Common Murre subcolony, the reduction in the proportion of birds breeding, and the delay in breeding in an adjacent Razorbill subcolony suggests that a fox may have visited this part of GC3 briefly. The location of the abandoned Common Murre subcolony and the adjacent Razorbill study plot are at the point closest to GC2 (see Fig. 1), so it is feasible that a fox crossed from there to GC3. The crossing may have been achieved by walking over concentrated pans

of ice or by swimming. Arctic foxes are apparently good swimmers (Nowak 1991), but on all but the calmest days the seasurface current between GC2 and GC3 would have probably deterred a fox from doing this. In fact, it seems unlikely that foxes swam between the islands, as we saw no sign of them doing so during our visit. A more likely scenario is that the presence of sea ice and its movements between the islands allowed foxes to make a brief visit to GC3 around mid-July and to leave from GC4 sometime earlier.

The Gannet Islands are all relatively low lying, with relatively few steep cliffs, and the maximum height of these is 66 m. As a result, all the alcid species, except for most of the Thick-billed Murres and a few Common Murres and Razorbills, breed in very accessible locations. This suggests that the occurrence of arctic foxes or other important terrestrial predators at this colony must be an extremely infrequent event. In other seabird colonies, areas where terrestrial predators occur regularly, such as mainland sites, most seabirds are forced to breed in inaccessible sites, usually in rock fissures or crevices or on steep vertical cliffs (Fisher and Lockley 1954, Freuchen and Salomonsen 1958, Larson 1960, Tuck 1961, Lack 1968, Salomonsen 1979, Petersen 1982, Bailey 1993).

The occurrence of arctic foxes at the Gannet Islands may have been a chance event associated with heavy winter ice and a low in the abundance of small rodents on the mainland: i.e., Ungava lemming cycle (Lewis 1923, Elton 1942, Harper 1960, Vibe 1967, Banfield 1974). Such a shortage in food availability is known to cause the foxes to undergo extensive movements and shift toward the coast and out onto the sea ice (Banfield 1974, Nowak 1991). In fact there was an arctic fox invasion along the north shore of the Gulf of St. Lawrence during the 1987–1988 winter (Canadian Wildlife Service-Quebec Region files) that subsequently adversely affected several seabird island sanctuaries within the region before they were removed (G. Chapdelaine, Can. Wildl. Serv., pers. comm.). Nearshore locations in coastal Labrador have more frequent visitations by foxes and other four-legged predators than those farther offshore such as the Gannet Clusters. However, the fact that in 1992 there were four adult foxes and one pair was breeding, suggests a resident and expanding population that may also be related to winter 1987–1988.

If the foxes are successful and remain on the Gannet Islands, most seabird species eventually will be eliminated, as has occurred on some of the Aleutian Islands and elsewhere in Alaska (Bailey 1993). This raises an interesting point regarding the life history strategies of long-lived seabirds. Our observations suggest that foxes may have been on GC2 and GC5 for one or more seasons prior to 1992, perhaps since the winter of 1987–1988. As far as we could tell, the adult Razorbills were still firmly

associated with their breeding subcolony, visiting sporadically, but spending a lot of time on the sea immediately adjacent to the subcolony. It is interesting to speculate how long a bird could afford to wait before deserting its subcolony and attempting to find a breeding site elsewhere. Presumably part of the answer to this question depends upon the availability of other nearby colonies or other locations where new colonies could start and the length of time the disturbance factor is likely to persist at the present site. It may be significant that most Razorbills were continuing to associate with the Gannet Islands, despite their inability to breed owing to the presence of foxes, simply because suitable alternative sites are extremely scarce or the foxes are unlikely to remain and disperse to islands within the Gannet Island archipelago. There are several reasons for thinking that one or both of these might be the case. The Gannet Islands are farther offshore than any other islands along this stretch of coast, a factor which may increase the foraging efficiency of the birds, but also provide them with a relatively high degree of safety from terrestrial predators, including people (for details, see Nettleship and Evans 1985). Short-term losses may be offset by gains over the longer term, especially if the foxes do poorly and cease to reproduce successfully, one consequence of which might be to abandon the islands during winter when conditions allow (Banfield 1974, Nowak 1991). The fact that the Gannet Islands seabird community has been known for more than a century and that foxes do not seem to be a regular part of the Gannet Islands' terrestrial ecosystem (based on existing information: no previous records of foxes—either direct observations or the presence of scats,—over a period of at least 70 years) suggest that conditions necessary for establishment of a permanent fox population on the Gannet Islands are deficient and that the present animals will soon disappear since there is no alternative prey other than a very small population of passerines during summer and a small population of deer mice (*Peromyscus maniculatus*) on GC4. The small litter size (2 instead of the usual 6–12, Nowak 1991) of the pair on GC2 and nonbreeding by those on GC5 support this prediction, though the pair on GC5 could both have been the same sex or infertile. After consultation with the Canadian Wildlife Service and the Newfoundland-Labrador Seabird Ecological Reserve Committee, it was decided that because of the status of the Gannet Islands, the foxes should be removed. Accordingly, in late September 1992, an adult female and two pups on GC2 and one adult of GC5 were shot under permit. A visit to GC2 and GC5 in May 1993 revealed that no foxes were present, nor were there any tracks in the snow or scats, which indicates that the remaining foxes had not remained or had failed to survive.

ACKNOWLEDGMENTS

This research was funded by research grants to D.N.N. from the Canadian Wildlife Service, Environment Canada, with additional financial support provided through the Comprehensive Labrador Cooperation Agreement, Happy Valley–Goose Bay, Labrador, to whom we are grateful. We thank Gary Glenn and Gary Burness for assistance in the field, Tony Elson and his crew on the MV *Blue Thunder,* Blair Gillis of Northern Stores (Cartwright), and Harry Martin of the Newfoundland Wildlife Division (Cartwright). We are also greatful to Roland Clark, Manuel Pardy, and the RCMP detachment in Cartwright, and to Donald Hustins and Glen Ryan of the Newfoundland and Labrador Department of Environment and Lands (Parks Division), for their support and interest in the project. We thank Edgar Bailey for reading an early draft of the manuscript, and George Divoky and Michael Gochfeld for providing helpful comments during the review process. This investigation is associated with the program "Studies on northern seabirds," Seabird Research Unit, Canadian Wildlife Service, Environment Canada, Dartmouth, Nova Scotia (Report No. 264).

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COLOR PLATE

Publication of the frontispiece painting by David Quinn has been made possible by an endowment established by George Miksch Sutton.

Wilson Bull., 107(3), 1995, pp. 413–422

MIGRATION CHRONOLOGY, SEX RATIO, AND BODY MASS OF LEAST SANDPIPERS IN BRITISH COLUMBIA

Robert W. Butler and Gary W. Kaiser[1]

Abstract.—We banded, weighed, and measured 2147 Least Sandpipers (*Calidris minutilla*) migrating across the Fraser River delta in 1977–1987 and Sidney Island in 1990–1993. The adult migration from late June to early August overlapped the juvenile migration between late July and late September. The mean body mass of adult females on their northward migration was not significantly greater than on their southward migration. Samples sizes of northward migrating males were too small to draw similar comparisons. Adults were not significantly heavier than juveniles on the southward migration. Mean body masses were greatest in the third week of July among adults and in the third week of August among juveniles. The average length of stay during migration was estimated to be about five days in autumn. *Received 24 Aug. 1994, accepted 10 Feb. 1995.*

The Least Sandpiper (*Calidris minutilla*) is one of the most numerous shorebird species on the Pacific Coast of North America during migration (Jewett et al. 1953, Page et al. 1979, Butler and Campbell 1987, Butler 1994). Its breeding range extends across the boreal forests and southern tundra of North America (Miller 1986, Cooper 1994). Small numbers breed on the Queen Charlotte Islands and in northwestern British Columbia (Campbell et al. 1990, Cooper 1993), but the majority of western populations of Least Sandpipers breed farther north in Alaska and Yukon (Godfrey 1986, Hayman et al. 1986). During the winter, Least Sandpipers are found along the Pacific coast from southern Washington to southern Peru (Hayman et al. 1986, Paulson 1993). Information is available on the seasonal occurrence, habitat use, and body mass of Least Sandpipers migrating in Ontario and Venezuela and on the winter quarters in California (Page and Bradstreet 1968, Page and Salvadori 1969, Bradstreet et al. 1977, Page et al. 1979, Thomas 1987). However, this information is lacking during migration along the north Pacific Coast. This paper describes the timing of the southward migration, body mass of age and sex classes, and the length of stay of Least Sandpipers in southwestern British Columbia.

METHODS AND STUDY AREA

We studied migrant Least Sandpipers on the Fraser River delta (49°05′N, 123°00′W) and on Sidney Island (48°40′N, 123°20′W) in extreme southwestern British Columbia. The Fra-

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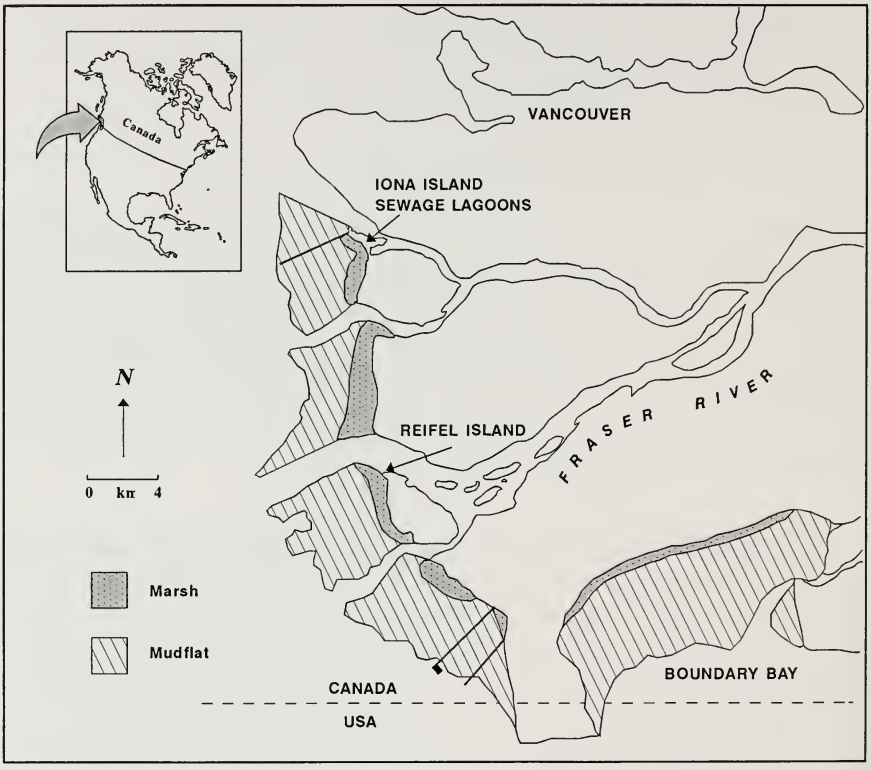

FIG. 1. Distribution of foraging habitats for Least Sandpipers in the Fraser River delta, British Columbia.

ser River delta has over 250 km^2 of mud and sandflat and about 0.4 km^2 of marsh is exposed during the lowest tide (Fig. 1, Butler and Campbell 1987). Marshes at the mouth of the Fraser River are dominated by plant species that can tolerate brackish and freshwater conditions. Boundary Bay marshes are dominated by saltmarsh plant species. Two sewage lagoons on Iona Island (Fig. 1) were used as a roost by large numbers of shorebirds during high tides. The lagoons were built behind 2 m-high dykes within 250 m of the marsh (Fig. 1). The study site on Sidney Island was a lagoon containing about 96 ha of mudflat, eelgrass beds, and saltmarsh (Butler et al. 1987).

On the Fraser River delta, sandpipers were caught during the periods of 10 May–10 June 1977, 7 June–15 November 1978, 4 May–9 September 1979, 7 July–9 September 1980, 5 July–28 August 1981, 9 July–1 September 1982, 5 July–10 September 1983, 7–16 August 1984, 4–24 July 1985, 27 July–23 August 1986, and 15 July–22 August 1987. On Sidney Island, Least Sandpipers were caught in the periods 1 July–31 August 1990–1993. Sandpipers were caught in mist nets strung across the beach and marshes for about 1–2 h on either side of high tides. On the Fraser River delta, we caught sandpipers at a sewage lagoon near brackish marshes on Iona Island, in brackish marshes on Reifel Island, and in salt marshes in Boundary Bay (Fig. 1).

TABLE 1

PROPORTION OF ADULT AND JUVENILE LEAST SANDPIPERS IN NET CATCHES ON THE FRASER RIVER DELTA DURING SOUTHWARD MIGRATION

Period	Number		Adult proportion
	Adult	Juvenile	
June 21–30	6	0	1.000
July 1–7	37	0	1.000
July 8–14	354	0	1.000
July 15–21	135	7	0.951
July 22–31	66	138	0.324
August 1–7	14	367	0.037
August 8–14	1	502	0.020
August 15–21	0	257	0.000
August 22–15 Sept.	3	235	0.013
Total	616	1506	0.290

Each bird was weighed within 0.5 h of capture with a Pesola spring balance, and its culmen was measured with a ruler. We used plumage characteristics to classify each bird as either adult (AHY) or juvenile (HY) (Prater et al. 1977). Least Sandpipers, can be sexed from measurements of their culmen lengths (Page 1974, Prater et al. 1977). Page (1974) derived his measurements of culmen lengths from 89 museum specimens of known sex collected on the Pacific Coast. Cooper's (1993) culmen measurements from 148 males and 135 females caught on nests on the Queen Charlotte Islands were nearly identical to Page's (1974) measurements from museum specimens (Page: mean = 17.9, SD = 0.7, 15.8–20.2 mm; Cooper; mean = 17.9, SD = 1.0, 15.5–20.4 mm). Therefore, we used Page's (1974) measurements of culmen lengths to assign sex of males (<17.5 mm) and females (>18.7 mm).

Individual differences in body mass were standardized as a proportion of body structural size by the expression $WT/C^{0.497}$, where WT is the body mass, C is the culmen length, and 0.497 is the slope of the fitted least-squares regression line between the logarithm of the culmen length and the logarithm of body mass (Summers 1988).

We used the method described by Butler et al. (1987) to estimate the length of stay of 155 Least Sandpipers. The Fraser River delta was too large to search for marked sandpipers each day, so we focused this work on the small study area on Sidney Island. Butler et al's (1987) length of stay method involves banding sandpipers with unique combinations of colored bands and searching for them each day through the migration period. The number of days lapsed between the banding date and the date of the last sighting is used as a minimum estimate of the length-of-stay.

RESULTS

Timing of age and sex classes during southward migration.—The earliest adult Least Sandpiper was caught on 26 June, and most had left by the end of July, although a small number were caught as late as 15 September (Table 1). The first juvenile was caught on 16 July, and most juveniles had departed by the middle of September. Small numbers of

TABLE 2
FREQUENCY DISTRIBUTION OF LEAST SANDPIPER CULMEN LENGTHS IN SOUTHWESTERN BRITISH COLUMBIA[a]

Culmen length (mm)	Number
<14.0	1
14.0–14.9	0
15.0–15.9	13
16.0–16.9	184
17.0–17.9	603
18.0–18.9	675
19.0–19.9	479
20.0–20.9	154
21.0–21.9	22
22.0–22.9	14
23.0–23.9	2
Total	2147

[a] Mean = 18.4, SD = 1.2, SE = 0.03, Range = 13.3–23.5.

juveniles were caught up to 11 November, when our study ended (Table 1). A small number of Least Sandpipers spend the winter on the Fraser River delta and elsewhere in southwestern British Columbia (Campbell et al. 1990).

Page's (1974) culmen measurements for males and females allowed us to sex 1280 (59.6%) of the 2147 sandpipers (474 males and 806 females, Table 2). The apparently skewed sex ratio probably was an artifact of the method of using culmen lengths to sex our sample. The mean culmen length in our sample of 2147 birds was 18.4 mm compared to 17.9 mm calculated by Page (1974) and Cooper (1993) from samples of 89 and 283 birds, respectively. This artifact might also explain the apparent decline we found in the weekly proportion of females captured during the migration of adults ($t = -21.7$, $r^2 = 0.97$, $P = 0.002$) and juveniles ($t = -14.6$, $r^2 = 0.99$, $P = 0.005$) (Table 3). The change in proportions of females in captures between the beginning and end of the migration period of adults and juveniles was about 10% (Table 3). Therefore, a small percentage of females incorrectly classified as males would explain these results.

Seventy-three of the 2147 Least Sandpipers captured on the Fraser River delta had longer culmens than the maximum length (20.4 mm) reported by Cooper (1993), and 100 were longer than the 20.2 mm maximum length reported by Page (1974). One bird had a culmen shorter than the minimum length (15.5 mm) reported by Cooper (1993), and 14

TABLE 3
PROPORTION OF ASSIGNED MALE AND FEMALE LEAST SANDPIPERS IN NET CATCHES ON THE FRASER RIVER DELTA DURING SOUTHWARD MIGRATION

Period	Number		Female proportion
	Male	Female	
June 21–30	1	4	0.800
July 1–7	7	16	0.696
July 8–14	82	139	0.629
July 15–21	33	41	0.554
July 22–31	48	80	0.625
August 1–7	79	162	0.672
August 8–14	118	215	0.646
August 15–21	64	98	0.605
August 22–15 Sept.	42	51	0.548
Total	474	806	0.630

were shorter then Page's (1974) minimum measurement of 15.8 mm. The respective probabilities that Page (1974) and Cooper (1993) would have missed a long billed Least Sandpiper if it occurred in the same proportion as in our sample (73 out of 2147) is very low and significant (Page: $P = (1 - (73/2147)^{89} = 0.05$; Cooper: $P = 1 - (73/2147)^{283} = 0.00006$). However, in our study, long billed birds were caught in each of the nine yrs that more than 50 Least Sandpipers were caught on the Fraser River delta and in the three years we sampled on Sidney Island. Moreover, the frequency of capture was similar on Sidney Island and the Fraser River delta; 3.4% (73 out of 2147) of the sandpipers caught on the Fraser River delta had long bills compared to three out of 154 sandpipers (2.3%) on Sidney Island. Lastly, the proportion of long billed sandpipers was nearly identical among adult (24/689 adults = 0.035) and juvenile age classes (49/1427 juveniles = 0.034). We conclude that a small number of Least Sandpipers on the Fraser River delta have longer bills than those reported by Page (1974) and Cooper (1993).

Body mass of age and sex classes.—Body masses of Least Sandpipers in our study ranged from 17 to 36 g. The mean mass of adult females was not significantly greater on their northward migration in May than during their southward migration in July, and adults were not significantly heavier than juveniles (Table 4). Larger samples are required to draw conclusions about body masses of adult males on the northward and southward migrations. Body masses of adults were significantly greater in the saltmarsh than in the riverine marsh and sewage lagoon (Table 5). Juveniles had significantly greater mass in the saltmarsh and riverine

TABLE 4
BODY MASS OF LEAST SANDPIPERS ON THE FRASER RIVER DELTA

Period	Adult				Juvenile			
	Mean	SE	N	Range	Mean	SE	N	Range
Spring								
Male	22.3	2.3	3	18–26		Not applicable		
Female	25.2	0.9	13	21–33		Not applicable		
Autumn								
Male	22.6	0.3	122	17–33	21.9	0.2	304	15–33
Female	24.3	0.2	196	20–33	23.8	0.2	529	15–36

marsh when compared to the sewage lagoon (Table 5). The mean body mass of adults was significantly greater than juveniles in the saltmarsh (Table 5).

The body mass of samples of Least Sandpipers increased significantly through the migration period of adults ($t = 2.1$, $P = 0.04$, $r^2 = 0.007$) and juveniles ($t = 4.0$, $P < 0.0001$, $r^2 = 0.011$; Fig. 2). The greatest mean mass occured in samples taken in the week of 15–21 July for adults and 22–31 August for juveniles (Fig. 2). The daily change in mass among eight Least Sandpipers that were recaptured was highly variable. Three birds lost body mass, one showed no change, and four birds increased in body mass between captures. The average change in mass of the eight recaptured Least Sandpipers was 0.22 g/d (SE = 0.15). In comparison, four Western Sandpipers (*C. mauri*) recaptured in the same period gained body mass at an average rate of 0.34 g/d (SE = 0.08).

Length of stay.—Of 155 color-marked Least Sandpipers on Sidney Island, 51 (32.9%) disappeared following banding, and the remaining 104

TABLE 5
STANDARDIZED BODY MASS INDICES (SEE METHODS) OF ADULT AND JUVENILE LEAST SANDPIPERS AT THREE LOCATIONS ON THE FRASER RIVER DELTA

Habitat	Adults			Juveniles		
	$\bar{x}$	SE	N	$\bar{x}$	SE	N
Sewage lagoon	5.308[a]	0.077	71	5.260[c]	0.042	320
Riverine marsh	5.459[b]	0.039	266	5.398[c]	0.034	469
Saltmarsh	5.619[b]	0.041	262	5.455[a]	0.032	569

[a] t-test $P < 0.001$.
[b] t-test $P < 0.01$.
[c] t-test $P < 0.02$.

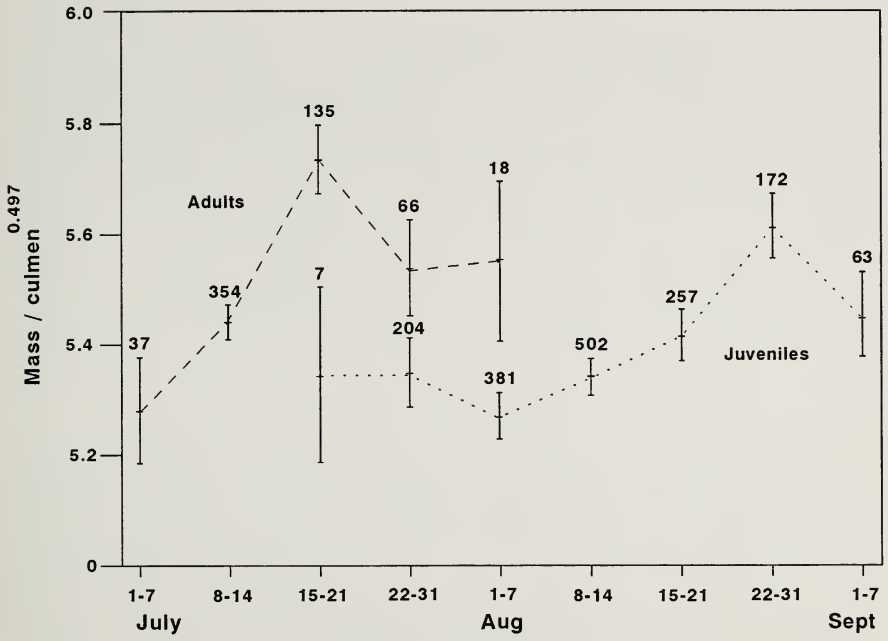

FIG. 2. Average standardized body mass of adult and juvenile Least Sandpipers during each week of the southward migration. Body size was standardized by dividing the mass by culmen raised to the power of 0.497. See Methods for details. Standard errors are represented by vertical bars and sample sizes appear above each sample.

were seen between one and 17 days later (Table 6). Using the methods described by Butler et al. (1987), we estimated P, the probability that a bird present the current day was present the next, and L, the expected length of stay. Our results are $P = 0.798$ and $L = 4.96$ (Table 6). This method provides a minimum estimate, because it includes birds that had already been present on the island for a few days before being caught and birds that fled as a result of capture.

DISCUSSION

The timing of southward migrations of age classes and sex classes of the Least Sandpiper through southwestern British Columbia was essentially the same as that of the Western Sandpiper. Adults of both species migrated mostly between the last week of June and the end of July, followed by juveniles from end of July to mid-September (this study, Butler et al. 1987). Our results concur with findings from migration studies of other calidridines in which the sexes generally migrate at slightly different times (Myers 1981, Butler et al. 1987). We found that females preceded

TABLE 6
NUMBER OF DAYS THAT MARKED LEAST SANDPIPERS WERE SEEN ON SIDNEY ISLAND[a]

Number of days	Number of individuals
1	155
2	104
3	90
4	75
5	66
6	59
7	46
8	42
9	39
10	27
11	23
12	15
13	13
14	7
15	3
16	3
17	1

[a] $S_k = 613$, $X_0 = 155$, $X_k = 0$, $\hat{P} = 0.7982$, var $(\hat{P}) = 0.0002$, SE$(\hat{P}) = 0.0145$, $\hat{L} = 5.0$; confidence intervals for $\hat{P}$ [0.7692, 0.8271]; confidence intervals for $\hat{L}$ [4.3, 5.9].

males during the adult and juvenile migrations. However, the accuracy of sexing Least Sandpipers using culmen lengths needs to be examined.

We showed that extremes in culmen lengths occurred regularly at low frequency among Least Sandpipers caught on migration in southwestern British Columbia. The origin of these Least Sandpipers is unknown. However, the scattered dates of occurrence in our catches, the presence among adult and juvenile cohorts, and their occurrence on the Fraser River delta and Sidney Island indicate that these individuals are widespread in Pacific Coast populations.

Least Sandpipers netted on their northward migration on the Fraser River delta were not significantly heavier than adults caught during the southward migration. This contrasts with the Western Sandpiper that migrates through the same habitats on the Fraser River delta at the same time of year. Adult Western Sandpipers were significantly heavier in spring than in fall (Butler et al. 1987). Many calidridines that breed in arctic environments carry large amounts of lipid and protein in spring to make the migration and survive inclement weather on the breeding grounds (e.g., Davidson and Evans 1988, Harrington et al. 1991). The Least Sandpiper breeds at the most southerly latitude of any North American calidridine (AOU 1983). We hypothesize that the Least Sandpiper

carries proportionately smaller nutrient reserves because it migrates shorter distances and does not need to contend with periodic food shortages that confront arctic breeding species.

The southward migration of individual Least Sandpipers was more protracted than that of the Western Sandpiper on Sidney Island. The average Least Sandpiper stayed about five days compared to about three days for the Western Sandpiper (Butler et al. 1987). Moreover, Least Sandpipers gained body mass at about two-thirds the rate of Western Sandpipers. We hypothesize that Least Sandpipers needed more time to increase their body mass and therefore remained on Sidney Island longer than Western Sandpipers.

ACKNOWLEDGMENTS

Many people assisted us in banding on the Fraser River delta. Prominent among them were David Alcroft, Scott Crawford, Kathleen Fry, John Ireland, and Terry Sullivan. Moira Lemon, Christopher Schmidt, and Terry Sullivan assisted on Sidney Island. Pam Whitehead prepared the figure, and G. E. John Smith provided statistical advice. We thank John Cooper, Bob Elner, Brian Harrington, Marshall Howe, Dov Lank, Dennis Paulson, and Steve Wetmore for comments that improved the manuscript.

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Wilson Bull., 107(3), 1995, pp. 423–436

COMMON TERNS NESTING ON NAVIGATIONAL AIDS AND NATURAL ISLANDS IN THE ST. LAWRENCE RIVER, NEW YORK

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Abstract.—We evaluated breeding success of Common Terns (*Sterna hirundo*) on natural and man-made islands (navigational aids or cribs) in the upper St. Lawrence River, New York, to ascertain the importance of man-made habitats for conservation. Terns nesting on man-made sites had greater hatching and fledging success, 1.78 chicks per pair in 1984 and 2.00 chicks per pair in 1986, compared to those nesting at natural sites, 0.01 and 0.00 chicks per pair in 1984 and 1986, respectively. The difference in overall breeding success was attributed to higher avian predation at natural than at man-made sites. Natural sites appeared to be unsuitable habitat, whereas man-made islands appeared to be suitable. Between 1982 and 1990, the St. Lawrence River Common Tern population increased by 13%.
Received 26 July 1994, accepted 1 March 1995.

The Common Tern (*Sterna hirundo*) breeds throughout the northern hemisphere of both the Old and New Worlds (Peters 1934, AOU 1983). In the upper St. Lawrence River (SLR), Common Terns were first observed in 1858 (Hadfield 1859). The first breeding record for upstate New York was noted in the SLR in 1917 (Merwin 1918). Subsequent reports suggest that there has been a continued occurrence of Common Terns in the upper SLR for more than 73 years (Courtney and Blokpoel 1983, Smith et al. 1984). Historical data for the period 1900–1982 indicate that the population was on the increase beginning in 1900, reached a peak of 1250 pairs in 1965 (Courtney and Blokpoel 1983, Smith et al. 1984), and then declined to an estimated 488 pairs by 1982 (Smith et al. 1984).

In other regions of the Great Lakes about 70% of terns nest at man-made sites. This shift from natural sites occurred as man-made sites became available through the 1970s and/or as natural sites were lost to a variety of abiotic and biotic factors (Courtney and Blokpoel 1983, Shugart and Scharf 1983). Our cursory observation in the SLR suggested a similar trend. Furthermore, it appeared that the present size of the population was now dependent on man-made navigation aids (cribs) that were constructed between 1973–1979. In this study, we document these observations.

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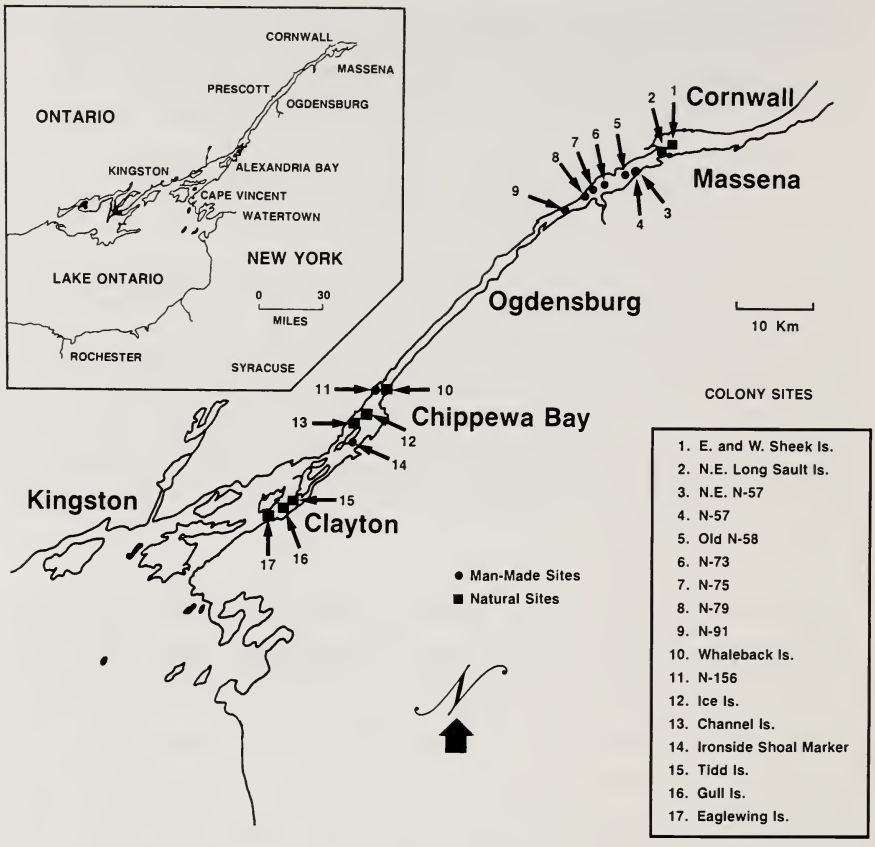

FIG. 1. Common Tern colony sites found along the upper St. Lawrence River, New York, in 1984.

STUDY AREA AND METHODS

We conducted this study in the 201-km long international sector of the St. Lawrence River between Clayton and Massena, New York (Fig. 1). Among the hundreds of islands and shoals in the study area, only 30 are historically known to have been used by nesting Common Terns (Courtney and Blokpoel 1983, Smith et al. 1984, Karwowski, pers. obs.). A total of nine natural islands were used in 1984, six of which were on the United States (U.S.) side of the river (Fig. 1). Of these sites, Eagle Wing Islands (EWI-1 and EWI-2) and Gull Island were selected for the study.

EWI-1 and EWI-2 are approximately 400-m^2, granitic-gneiss, rock outcroppings located 3300 and 2300 m, respectively, from the nearest mainland. Herbaceous vegetation typically grew in the very shallow, low lime, loamy soil that accumulated in the cracks and depressions of the rock (McDowell 1989). EWI-1 rises gently from water level on the east end to a maximum height of about 2.5 m on the steep west end. In contrast, EWI-2 rises gently

from all sides to a maximum level above water of about 1 m. Both islands are prone to some over-spray and wash-over, i.e., flooding, from waves generated during strong winds.

Gull Island is a 800-m^2, granitic-gneiss rock outcropping located about 3 km east of the EWIs and 1700 m from the nearest mainland. The southern end of the island rises abruptly to about 6 m above water level and forms a flattened dome covering nearly 33% of the island. The remainder is relatively flat, rising about 1.5–2.0 m above water level and sloping gently toward the river. Thin (approx. 4 cm in depth) soil occurs in the central portion of the island, on the top of the "dome," and in cracks and depressions. It supports grasses, forbs, shrubs, and small trees. Gull Island is not exposed to wave-generated over-spray or wash-over.

Nineteen navigation aids are located in U.S. waters and are owned and maintained by the U.S. Dept. of Transportation, St. Lawrence Seaway Development Corporation, Massena, New York. All navigation aids are structurally similar and stand on the river bottom. Each marker consists of a cylindrical steel base, 8 m in diameter, that is partially filled with concrete, gravel, or soil, and a metal scaffolding that supports one or more types of navigation instruments. The surfaces are approximately level (forming a platform) with the upper rim of each base located about 2.5 m above mean water level. The height of the upper rim from the core substrate differs within and among the sites and ranges from 5–33 cm. Scaffolding is located at the center of each marker and ranges in height from 5–9 m.

In 1984 and 1986, eight markers were used by nesting terns (Fig. 1). Of these, we selected navigation light number 156 (N-156) and the Cat Island Shoal steering light (N-58) for intensive study. N-156 and N-58 had been filled with dredged river sediment that supported a moderately dense, herbaceous cover that uniformly covered the surfaces of both navigation aids. The surface area of both navigation aids was 50.3 m^2 and the distance from the substrate to the upper lip of the sheet piling ranged from 5–23 cm at N-156, and was 5 cm at N-58. N-156 and N-58 are located 3750 and 1050 m from the mainland, respectively.

In 1984, we studied breeding success and nest site habitat at EWI-1, EWI-2, Gull Island, and navigation aids N-156 and N-58. In 1986, we did a less intensive study of breeding success at EWI-1, EWI-2, Gull Island, and navigation aid N-156. We also collected data on the numbers of nesting terns and evidence of mortality at all active colonies during the period 1982–1990.

From mid-May to mid-July 1984 and 1986, we visited each colony daily by boat, except when prevented by rain. To minimize disturbance at the colonies, we limited our visits to ≤30 min and scheduled them during periods of moderate temperature and no precipitation. We marked all nests with a numbered stake and kept a detailed chronology on each nest and its contents until the last egg hatched or the nesting attempt failed, except in 1986, we marked a random sample of 22 nests at site N-156 for study. Egg fates were determined and reported using one of the following definitions: hatched—egg hatched; depredated—egg known to have been eaten or destroyed by predators or egg disappeared before it could have hatched; abandoned—egg left in nest no longer incubated by adults; died while pipping—egg began to hatch, but the chick did not emerge; flooded—egg in nest inundated with water or washed out of the nest by waves; failed to hatch—egg failed to hatch with others in the clutch or was incubated beyond 35 days; other—egg not retrieved from outside the nest, broken egg, or broken by investigators. Using 7 × 50 binoculars from a boat positioned 70–100 m offshore, we observed each colony site for night desertions on four separate dates. Dawn and dusk observations were made for one h beginning 30 min prior to sunrise and sunset, respectively, to determine night desertion and/or morning arrival behavior (Marshall 1942). We also measured incubation attentiveness for use as an indication of relative disturbance by determining the number of days clutches were incubated from

their initiation to the hatching of the first egg, and compared mean incubation periods among sites.

Prior to eggs hatching, we erected a 30-cm-high, 2.5-cm hexagonal mesh wire fence around the perimeter of each navigation aid. The fence prevented chicks from prematurely jumping off the navigation aid into the river in response to our presence. As erected, they would have little effect in deterring avian predators. Once in the river, chicks would not have been able to return to the navigation aid. The natural islands gently sloped toward the edge of the river; consequently, fencing was unnecessary as chicks entering the water could easily return to the island. Chicks were banded within two days of hatching with a U.S. Fish and Wildlife Service leg band.

We determined chick survival on each visit by completely searching the colony and recording all chick encounters. This method was facilitated by the small size and relatively sparse vegetation on the sites. Chicks that were not found on a given visit were usually found (>96%) during the next visit. Unless missing chicks were found during later visits, they were assumed to have been depredated. We considered chicks alive more than 18 days to have fledged, because after that time chicks could escape the enclosure on the navigation aids (Smith et al. 1984). We collected information on the fate of each chick until it died, disappeared, or was considered to have fledged (>18 days old).

We defined (a) hatching success for nests as the number of eggs hatched per eggs laid, (b) fledging success for nests as the number of chicks fledged per eggs hatched, and (c) breeding success for colonies as the number of young fledged per breeding pair, i.e., nest, for each colony. To evaluate hatching success and fledging success with respect to nest-site characteristics, we recorded in 1984 at the time the first egg hatched vegetation cover (%) and height (cm) within a 50-cm-radius, circular plot centered over the nest (Blokpoel et al. 1978); substrate beneath nest (soil, grass, gravel, or bedrock); number of neighboring nests within a 1-m radius of the nest; and distance (m) to nearest neighboring nest.

To evaluate the association of the observed shift in nesting habitat with the status of the Common Tern population, we compiled all available tern nesting data for the area from 1982–1990. The primary sources of data were observations by KK (1982–1990), LHH (1990 unpubl. data), and G. A. Smith (1982–1989 unpubl. data). In both 1984 and 1986, five visits were made by boat to every active Common Tern colony within the SLR at two-week intervals beginning around 22 May in each year. On each visit, an effort was made to count all nests in every colony. Colony size was determined by counting the number of nests at peak incubation to avoid counting renesting terns. Presence or absence of predation and relative hatching and fledging success were noted at all active sites. To determine if new colony sites had gone undetected, two complete searches of the river for new colonies were conducted in 1984 and 1988.

Nonparametric statistical procedures were used in data analyses because the assumptions of normality and homogeneity of variance could not be met. Chi-square (χ^2) tests for two independent samples, Wilcoxon-Mann-Whitney test, and Kruskal-Wallis one-way analysis of variance were used to compare clutch sizes, incubation attentiveness, hatching and fledging success, and egg fates within and among colonies. When the values of the Kruskal-Wallis test were significant ($P < 0.05$), we tested the significance of difference between colony sites using the multiple comparisons test described by Siegel and Castellan (1988). To examine the relationships among the nest-site variables measured in relation to hatching and fledging success, we used hierarchical log-linear analysis (HILOGLINEAR, SPSS/PC, V3.1) using backward elimination to test for significant interactions (Norusis 1985).

RESULTS

Breeding success and nest site characteristics.—The modal clutch size for all sites in 1984 and 1986 was three eggs, but larger clutches (four

TABLE 1

CLUTCH SIZE DISTRIBUTION, CLUTCH SIZE, AND LENGTH OF INCUBATION (MEAN ± SE) AMONG COMMON TERN COLONIES IN THE UPPER ST. LAWRENCE RIVER, NEW YORK, 1984 AND 1986[a]

Year	Colony	Clutch size distribution				Clutch size	Incubation (days)
		4	3	2	1		
1984	EWIs	0	34	6	5	2.64 ± 0.10 (45)A	30.3 ± 1.65 (6)A
1984	Gull Island	0	43	6	5	2.70 ± 0.09 (54)A	31.2 ± 0.49 (5)A
1984	N-156	0	59	0	5	2.84 ± 0.07 (64)A	23.5 ± 0.61 (13)B
1984	N-58	2	108	9	2	2.91 ± 0.04 (121)A	22.9 ± 0.31 (14)B
1986	EWIs	1	44	12	7	2.61 ± 0.09 (64)A	29.7 ± 1.86 (3)A
1986	Gull Island	0	22	2	9	2.39 ± 0.16 (33)A	31.2 ± 0.39 (13)A
1986	N-156	16	32	4	2	3.15 ± 0.10 (54)A	22.4 ± 0.26 (8)B

[a] Significant differences between colonies in each year are shown by differences in letters within each column (nonparametric multiple comparison method, $P < 0.05$). Sample sizes are in parentheses.

eggs) were found in both years. Clutch sizes did not differ among the sites in either year (Table 1), but incubation attentiveness by adult terns did. In both years, incubation length was longer at colonies on natural sites than on man-made sites (Table 1).

In 1984, hatching success and the number of eggs hatched per nest at the man-made sites (for all nests with different clutch sizes pooled) differed significantly from that at the EWIs, but not from that at Gull Island (Table 2). In 1986, hatching success and the number of eggs hatched per nest at N-156 were significantly higher than at either natural site. Both hatching success and the number of eggs hatched per nest also differed between Gull Island and the EWIs, being higher at Gull Island (Table 2).

Large clutches (3–4 eggs) had significantly higher hatching success than small clutches (1–2 eggs) at both natural sites and at N-156 during 1984 (Table 3). In 1986, large clutches had higher hatching success at Gull Island, whereas all clutch sizes experienced low hatching success at the EWIs. No clutch size comparisons were made at N-156 during 1986, because all clutches in our random sample contained three eggs (Table 3).

A comparison of the number of eggs hatched by habitat type in 1984 and 1986 showed that nests on the man-made sites had more eggs hatch than expected, whereas nests on natural sites had fewer eggs hatch than expected (Chi-square test for two independent samples; $\chi^2 = 129.24$, df $= 6$, $P < 0.001$ and $\chi^2 = 117.57$, df $= 5$, $P < 0.0001$, respectively). Partitioning of the Chi-squares showed that in 1984, the frequencies of egg predation, abandonment, flooding, and chicks that died while pipping were higher for nests on natural sites and lower for nests on man-made

TABLE 2

MEASURES OF BREEDING SUCCESS (MEAN ± SE) AMONG COMMON TERN COLONIES IN THE UPPER ST. LAWRENCE RIVER, NEW YORK, 1984 AND 1986[a]

Year	Colony site	Hatching success	No. eggs hatched per nest	Fledging success[b]	No. chicks fledged per nest with hatched eggs	No. chicks fledged
1984	EWIs	0.41 ± 0.07 (43)A	1.19 ± 0.20 (43)A	0.00 ± 0.00 (21)A	0.00 ± 0.00 (21)A	0
1984	Gull Island	0.76 ± 0.05 (51)B	2.16 ± 0.16 (51)B	0.02 ± 0.02 (41)A	0.04 ± 0.04 (41)A	2
1984	N-156	0.91 ± 0.03 (57)B	2.72 ± 0.10 (57)B	0.68 ± 0.04 (43)B	1.87 ± 0.14 (43)B	84
1984	N-58	0.93 ± 0.02 (109)B	2.75 ± 0.05 (109)B	0.61 ± 0.03 (82)B	1.69 ± 0.10 (82)B	142
1986	EWIs	0.09 ± 0.03 (64)A	0.23 ± 0.09 (64)A	0.00 ± 0.00 (7)A	0.00 ± 0.00 (7)A	0
1986	Gull Island	0.46 ± 0.09 (33)B	1.33 ± 0.25 (33)B	0.09 ± 0.09 (11)A	0.11 ± 0.17 (11)A	3
1986	N-156	0.92 ± 0.04 (22)C	2.77 ± 0.11 (22)C	0.74 ± 0.06 (22)B	2.00 ± 0.17 (22)B	44

[a] Significant differences between colonies in each year are shown by differences in letters within each column (nonparametric multiple comparison method, $P < 0.05$). Sample sizes are in parentheses.

[b] Chicks survived >18 days.

TABLE 3

HATCHING AND FLEDGING SUCCESS (MEAN ± SE) OF 1–2 AND 3–4 EGG CLUTCHES AT COLONY SITES IN THE UPPER ST. LAWRENCE RIVER, NEW YORK, 1984 AND 1986[a]

Year	Colony	Clutch size	Hatching success	Fledging success[b]
1984	EWIs	1–2	0.18 ± 0.08 (11)	0.00 ± 0.00 (4)
		3–4	0.49 ± 0.08 (32)*	0.00 ± 0.00 (17)NS
1984	Gull Island	1–2	0.45 ± 0.14 (10)	0.00 ± 0.00 (6)
		3–4	0.82 ± 0.05 (41)**	0.02 ± 0.02 (35)NS
1984	N-156	1–2	0.00 ± 0.00 (3)	— (0)
		3–4	0.96 ± 0.02 (54)**	0.68 ± 0.04 (43)[b]
1984	N-58	1–2	0.72 ± 0.15 (9)	0.33 ± 0.33 (3)
		3–4	0.96 ± 0.01 (100)NS	0.62 ± 0.03 (79)NS
1986	EWIs	1–2	0.10 ± 0.07 (19)	0.00 ± 0.00 (2)
		3–4	0.08 ± 0.04 (45)NS	0.00 ± 0.00 (5)NS
1986	Gull Island	1–2	0.09 ± 0.03 (11)	0.00 ± 0.00 (1)
		3–4	0.64 ± 0.14 (22)**	0.10 ± 0.10 (10)NS
1986	N-156	1–2	— (0)	— (0)
		3–4	0.92 ± 0.04 (22)[c]	0.37 ± 0.06 (22)[c]

[a] The Wilcoxon-Mann-Whitney test for two independent samples was used to test for differences. Sample sizes are in parentheses.

[b] Chicks survived >18 days.

[c] Comparison was not made since all nests in the random sample contained three eggs.

* $P < 0.05$, ** $P < 0.01$, NS—not significant.

sites ($\chi^2 = 47.66$, $P < 0.0005$; $\chi^2 = 21.69$, $P < 0.001$; $\chi^2 = 52.51$, $P < 0.0005$; and $\chi^2 = 5.77$, $P < 0.02$; respectively). In 1986, the frequency of egg predation, nest abandonment, and flooding were higher than expected for nests on natural sites and lower than expected on man-made sites ($\chi^2 = 97.40$, $P < 0.0005$; $\chi^2 = 7.66$, $P < 0.01$; and $\chi^2 = 7.49$, $P < 0.01$; respectively).

The significantly greater hatching success at the man-made sites in 1984 was not explained by the data for the measured nest site characteristics. The relationships among the habitat measurements and hatching success were not statistically significant (HILOGLINEAR, $\chi^2 = 171.153$, df = 172, $P > 0.05$, all $z < 1.96$, $P > 0.05$).

Colonies at man-made sites produced significantly more young per nest than did the colonies at natural sites (Table 2). We found no difference in fledging success between small (1–2 eggs) and large (3–4 eggs) clutches (Table 3). Overall, the terns at natural sites experienced near total reproductive failure in both years, and the terns at the EWIs colony did not fledge young in either year (Table 4). In 1984, 68% of all chicks produced at the Gull Island colony were taken by predators, and 30% died in or at their nests. At the EWIs colony, 88% of the chicks produced

TABLE 4

SUMMARY OF CHICK FATES FOR COMMON TERN COLONIES STUDIED IN THE UPPER ST. LAWRENCE RIVER, NEW YORK[a]

	1984				1986		
Chick fates	Eagle Wing islands	Gull island	N-156	N-58	Eagle Wing islands	Gull island	N-156
Chicks hatched	51	110	155	300	15	44	61
Confirmed fledged	0	2	84	142	0	3	44
Presumed depredated	45	60	0	0	15	35	0
Died on site	6	33	14	28	0	6	0
Presumed fledged	0	2	141	172	0	3	61
Chicks fledged per nest with hatched eggs[b]	0.00 ± 0.00 (21)	0.04 ± 0.04 (41)	1.87 ± 0.14 (43)	1.69 ± 0.10 (82)	0.00 ± 0.00 (7)	0.11 ± 0.11 (11)	2.00 ± 0.17 (22)
Chicks fledged per nest with eggs[b]	0.00 ± 0.00 (43)	0.04 ± 0.04 (51)	2.20 ± 0.16 (57)	1.42 ± 0.09 (109)	0.00 ± 0.00 (64)	0.09 ± 0.08 (33)	[c]
Age at disappearance in days	4.5 ± 0.52 (45)	2.2 ± 0.29 (60)	—	—	3.9 ± 1.08 (15)	3.9 ± 0.40 (41)	—
Age at death (days)	2.5 ± 0.22 (6)	3.4 ± 0.59 (33)	8.6 ± 1.36 (14)	3.5 ± 0.46 (16)	—	2.3 ± 0.33 (3)	—

[a] Means (±SE) are presented where appropriate. Sample sizes are in parentheses.
[b] Fledged means chick survived >18 days.
[c] Could not be determined from the subsample data.

were taken by predators and the remainder (12%) died in their nests. The fate of chicks at both natural sites was similar in 1986. Eighty-five percent of the chicks produced at Gull Island and 100% of the chicks at the EWIs colony were depredated. In addition, 15% of the chicks at Gull Island were found dead near their nests.

Based on direct observation and circumstantial evidence at the natural sites, we believe that Great Horned Owls (*Bubo virginianus*) in the SLR caused the direct loss of Common Tern adults and pre-fledgling chicks and the indirect loss of pipping eggs and newly hatched young to exposure resulting from nocturnal nest desertion by adults. No signs of predation or nocturnal nest desertions were observed at the man-made sites. Our observations of night desertion and morning arrival behavior indicated that adult terns often deserted the natural islands for 6.5–8 h. We also observed a Great Horned Owl on the EWIs just after sunrise and, consistent with owl predation, found owl feathers, decapitated chicks, and wings, bills, and feathers of adult terns at every visited natural site.

HILOGLINEAR analysis of fledging success in relation to the habitat variables measured in 1984 produced a final model which contained statistically significant second-order interactions between fledging success and nest density. Nests which failed to fledge any young were associated more frequently than expected with nest densities in the categories low (1–4 nests) density ($\lambda = -0.0726$, $z > 3$, $P < 0.01$) and medium (5–8 nests) density ($\lambda = -0.3924$, $z > 2$, $P < 0.05$), than those in the category high density (>8 nests).

Shifts in nesting habitat use and population trends.—In 1976, Common Terns were observed for the first time nesting on a navigation aid (van Riet, pers. comm.). From 1977 to 1980, at least two navigation aids were used by nesting terns. By 1982, eight navigation aids were being used for nesting (Smith, unpubl. data; Karwowski, pers. obs.) (Fig. 2). Sites N-57, N-58, N-73, N-75, and N-79 were colonized within 1–3 years after their installation. Site N-156 was first known to be used within six years of its construction, N-180 was colonized within 15 years, and N-91 was colonized 18 years after being placed in the river.

Prior to 1982, nine natural sites which were known to have been used by nesting Common Terns (Bull 1974, Blokpoel 1977, Karwowski and Smith, unpubl. data) became unusable. Five sites (Black Ant, Scorpion, West Bergen, Bogardus, and Murray islands) were taken over by earlier nesting Ring-billed Gulls (*Larus delawarensis*). Two sites (Big and Little Murphy islands) became overgrown with vegetation. Between 1982 and 1990, five additional sites were eliminated from the pool of available tern nesting sites. Ice Island, historically the largest natural colony site, was taken over by Ring-billed Gulls; West Sheek Island was destroyed by

flooding and erosion; Old Man Island was overgrown with vegetation; and East Sheek Island, Stovin Island, and Sheaffle Island shoal were not used for unknown reason(s). The number of colonies on natural islands declined from a high of 11 in 1982 to a low of six in 1990 (Fig. 2).

In 1982, over 37% (181 out of 488 nests) of the tern breeding population nested on navigation aids (Fig. 2). By 1990, the use of navigation aids by nesting terns had increased to nearly 70% (384 out of 557 nests), with most concentrated at N-58, N-73, N-75, N-79, and N-156. Between 1982 and 1990, the number of nesting terns increased an average two percent annually, resulting in an overall increase of about 13% for the period. During this period, the population size averaged 546 (±12 SE) breeding pairs and ranged from a low of 488 in 1982 to a high of 596 in 1989 (Fig. 2). Although there has not been a major increase in the total number of nests of Common Terns from 1982 to 1990, there has been a decline in numbers of nests on natural islands with a corresponding increase in numbers on navigation aids. As the number of nests per colony on natural islands has not changed appreciably, the decline on natural islands has been due primarily to site abandonment. In comparison, the increase in nests on navigation aids has been due mainly to higher densities of nests rather than to an increase in number of navigation aids used by terns.

DISCUSSION

Both direct and indirect effects of predation were discernible at the natural sites, but not at the man-made sites, and accounted for the substantially higher breeding success of terns nesting at the man-made sites. The consequences of avian predation at Common Tern colonies are well documented (e.g., Nisbet 1975, Hunter and Morris 1976, Nisbet and Welton 1984, Morris and Wiggins 1986). The principal avian predator of adult Common Terns in North America is the Great Horned Owl. Predators of tern eggs and/or young include Black-crowned Night-Herons (*Nycticorax nycticorax*), Ruddy Turnstones (*Arenaria interpres*), Herring Gulls (*Larus argentatus*), and Canada Geese (*Branta canadensis*) (Courtney and Blokpoel 1980, Morris and Wiggins 1986, Burger and Gochfeld 1991). Ruddy Turnstones were observed puncturing and eating tern eggs (typically between 20–29 May), but their overall contribution to egg losses was not

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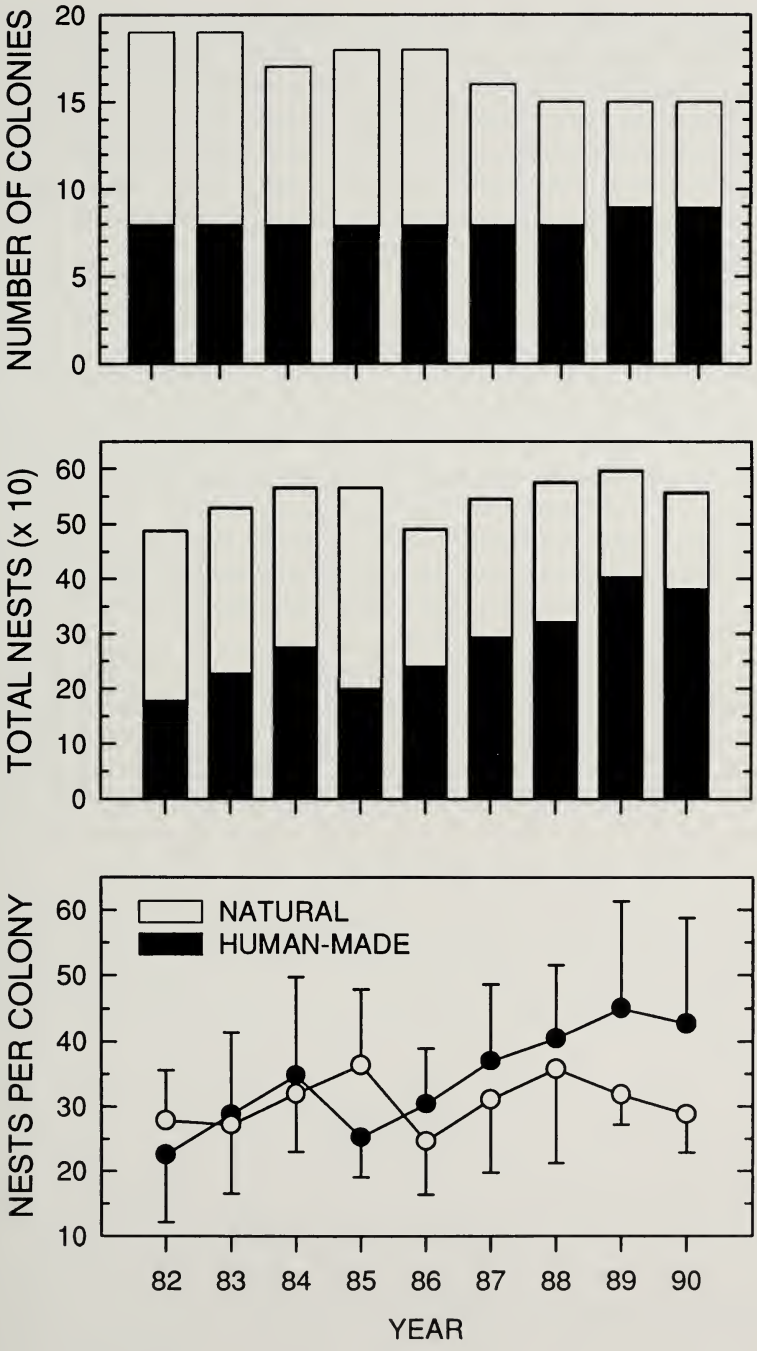
FIG. 2. Number of colonies, total nests, and mean (±SE) number of nests per colony on man-made and natural sites from 1982–1990 in the upper St. Lawrence River, New York.


NUMBER OF COLONIES
20
15
10
5
0
TOTAL NESTS (x 10)
60
50
40
30
20
10
0
NESTS PER COLONY
NATURAL
HUMAN-MADE
60
50
40
30
20
10
82
83
84
85
86
87
88
89
90
YEAR

quantified. In addition, two suspected predators of eggs and chicks were Great Blue Herons (*Ardea herodias*) and Black-crowned Night-Herons. Although we have no direct evidence, their contributions to egg and chick losses may have been substantial. Indirect losses were a consequence of nocturnal desertion of the sites by the adults, which was observed following the depredation of adult terns. The significantly longer incubation lengths and numbers of eggs which died pipping or that were abandoned are clear indicators of parental neglect.

Common Terns nesting in the SLR at natural sites undoubtedly have had a long history of exposure to Great Horned Owl predation (Waltz, pers. comm.). Because owls are highly territorial and nest-site tenacious (Craighead and Craighead 1969), high predation pressure at a tern colony in one year likely would be a good predictor of high predation pressure in subsequent years. Terns at colonies faced with avian predation certainly would have the opportunity to avoid predation in subsequent nesting attempts or years by using alternate colony sites. Owls would then stop visiting the former site because there would be no prey. It is likely that terns would continue to nest at the alternate site until predators discovered them. A colony would then move to another site that would be usable for a few years until discovered again.

Between 1982 and 1990, the natural and man-made sites used by nesting Common Terns were subjected to differing environmental conditions, which may have ultimately affected their suitability as tern nesting habitats. At the natural sites, terns were faced with high rates of predation, nest-site competition, risk of nest flooding, vegetation succession, and/or human disturbance (Smith et al. 1984; Karwowski, pers. obs.). Terns faced with high predation pressure had fewer choices of suitable, alternate nest sites. Some terns may have remained at sites which had high predation pressures due to colony- and nest-site fidelity (see Patton and Southern 1978, Southern and Southern 1979), whereas some individuals may have attempted to nest at novel sites to avoid predation, despite the potential for reducing their breeding success (McNicholl 1975, Erwin et al. 1981).

Terns nesting on navigation aids must have found nesting conditions to be quite different from those on natural islands. Unlike at natural sites, at man-made sites we found no evidence of depredation of eggs, chicks, or adults (e.g., perforated eggs, shell fragments, lengthened incubation periods, night desertion, or parts of chicks or adults). Distances of navigation aids and natural islands from the mainland were not significantly different (Karwowski and Gates, unpubl. data), so owls should have had no problem in reaching navigation aids. Perhaps owls were deterred by the scaffolding of the navigation aids. Interspecific competition for nest

sites also did not occur. Ring-billed Gulls have never been observed nesting on navigation aids, possibly because they have experienced no selective pressures to use them. Nests were not exposed to flooding because the nesting substrates were about 3 m above water level and well drained. All sites supported early successional vegetation preferred by nesting terns (Blokpoel et al. 1978). Furthermore, human disturbance such as recreational fishing or sight-seeing was rarely observed. Because of the high fledging success, these initial colonists and their offspring would likely have chosen to nest on navigation aids in the future.

Assuming that the upper SLR population is discrete with little or no movement to or from other areas, as reported for the Great Lakes population (Courtney and Blokpoel 1983), and that the rate of mortality outside the study area is comparable to other areas such as Massachusetts (Nisbet 1978) and Great Gull Island, New York (DiCostanzo 1980), a reasonable prediction about the long-term effects of the shift in habitat use by nesting terns on the size of their future breeding population can be made. The greater breeding success of Common Terns nesting at man-made sites and the increasing number of terns using those sites annually strongly suggest continued breeding population stability or increases on the SLR. Without active management of natural islands (Morris et al. 1992), tern colonies on the man-made sites likely will continue to be source populations for what would otherwise be a declining regional population. Because tern populations are so dependent upon these man-made sites for successful nesting, annual monitoring should be done to confirm their continued success and to address any potential problems that might arise.

ACKNOWLEDGMENTS

Special thanks go to B. Karwowski for the use of his boat; M. McMahon for his assistance in the field; and G. Maxwell and G. Smith for their interests and for introducing K.K. to Common Terns and the St. Lawrence River. Many thanks also go to H. Blokpoel, G. L. Brewer, J. Hickey, J. H. Howard, and J. E. McKearnan for their useful suggestions on the manuscript. We especially thank the St. Lawrence Seaway Development Corporation for giving us access to navigational aids. This is Contribution No. 2582-AEL, Center for Environmental and Estuarine Studies.

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Wilson Bull., 107(3), 1995, pp. 437–451

FORAGING SOCIABILITY OF NESTING WADING BIRDS (CICONIIFORMES) AT LAKE OKEECHOBEE, FLORIDA

Jeff P. Smith[1]

Abstract.—From 1989–1992 at Lake Okeechobee, Florida, I followed 356 adult Great Egrets (*Casmerodius albus*), 236 Snowy Egrets (*Egretta thula*), 82 Tricolored Herons (*E. tricolor*), and 286 White Ibises (*Eudocimus albus*) from several nesting colonies to foraging sites during chick-rearing periods. White Ibises departed in groups more often than the other species (64% of the birds followed), tended to travel in larger groups, rarely landed in areas devoid of other birds, and tended to join larger, more concentrated feeding flocks than other species. A majority of all species joined other birds at foraging sites. However, Great Egrets and Tricolored Herons often landed in areas devoid of other birds (29% and 43% of the birds, respectively) and more often landed near rather than in the immediate vicinity of other birds. A tendency toward group departures has been interpreted as support for the "information-exchange" hypothesis about the benefits of colonial nesting relative to food-finding. However, many of the birds in this study that departed in groups dispersed before landing, which is contrary to the expectations of the hypothesis. Many individuals did, however, choose foraging sites already occupied by other birds, which is indicative of reliance on "local enhancement" for identifying productive foraging grounds. Differences in degree of sociability among the species may, however, primarily reflect differences in foraging strategy. White Ibises are more social probably because foraging in groups enhances the effectiveness of the grope-foraging technique they employ, whereas Tricolored Herons and Great Egrets often employ foraging techniques more suited to solitary effort and are not as likely to benefit from foraging in aggregations. The evidence also suggested that Snowy Egrets, in particular, act as attractors for other species that rely on local enhancement to identify profitable foraging opportunities. This association may result from a combination of factors; i.e., white plumage serves as an attractor, but flocks of Snowy Egrets may also be particularly indicative of high-quality habitat and/or concentrations of universally attractive prey species. *Received 29 Aug. 1994, accepted 1 Feb. 1995.*

Researchers often have debated the issue of whether or not species benefit from colonial nesting because individual birds can exploit conspecifics or similar species for information about profitable foraging locations (Ward and Zahavi 1973, Krebs 1974, Ogden 1978, Custer and Osbom 1978, Pratt 1980, Erwin 1983, Waltz 1983). Ward and Zahavi (1973) initiated the concept of information-sharing at colonies; i.e., birds departing without prior knowledge of profitable foraging grounds may reduce their search time and gain advantage by following other birds to foraging grounds. Observation of birds traveling in groups from colonies was considered corroborating evidence. However, Erwin (1983) noted that

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individual birds might simply follow busy flight lines to "popular" foraging grounds and, therefore, not actually have to travel with other birds to gain advantage from colonial nesting. An extension of these ideas is the concept of local-enhancement (Krebs 1974, Kushlan 1977, Caldwell 1981, Erwin 1983, Master 1992). This theory holds that among species constrained by the demands of central-place foraging (sensu Orians and Pearson 1979) and the unpredictability of patchily distributed prey, colonial nesting increases foraging efficiency because individual birds can follow active flight lines or search commonly exploited areas and locate currently profitable patches of foraging habitat by cueing on the presence of other birds. A pronounced tendency to join other birds at feeding sites is taken as evidence of such a phenomenon.

Another issue related to the concept of local enhancement concerns whether or not certain species act as attractors in group-feeding situations. Several researchers have noted that highly visible white species such as Snowy Egrets (*Egretta thula*) and White Ibises (*Eudocimus albus*) often appear to attract other species (Armstrong 1970; Willard 1977; Kushlan 1977, 1978a, 1979; Caldwell 1981; Master 1992). However, Caldwell demonstrated using models that Snowy Egrets served as attractors for Tricolored Herons (*Egretta tricolor*), but Great Egrets (*Casmerodius albus*)—also white—did not. Thus, other aspects of the species' ecology may be involved, such as relative tendencies toward aggregation and/or differences in species' prey and foraging-habitat preferences.

In conjunction with a comprehensive study of the nesting and foraging ecology of wading birds at Lake Okeechobee, Florida (Smith and Collopy 1995, Smith et al. 1995), I monitored the foraging habits of nesting adults of four species during chick-rearing periods through aerial following-flights (also see Smith 1995). The demand for efficient foraging by adults peaks during the chick-rearing phase (e.g., Kahl 1964, Kushlan 1981). Therefore, evidence of reliance on mechanisms that facilitate efficient habitat selection should be particularly pronounced at such times. The four study species were Great Egrets, Snowy Egrets, Tricolored Herons, and White Ibises, all species that commonly nest in large mixed-species colonies at the lake (Smith and Collopy 1995, David 1994a). Herein, I examine species' propensities for traveling in groups and for joining other birds at feeding sites. I present data on the size and composition of the feeding assemblages each species joined, including a comparison of species' tendencies to join conspecifics versus other species. I also discuss how differences in degree of sociability may reflect differences in each species' foraging behavior.

STUDY AREA AND METHODS

Study area.—Lake Okeechobee is the third largest freshwater lake in the United States (1732 km^2 surface area) and is classified as subtropical and eutrophic (Aumen 1995). It drains a watershed of nearly 12,000 km^2, primarily through the Kissimmee River from the northwest, and is situated upstream of the remnant Everglades and Florida Bay (Fig. 1). Management of the lake and its resources gamers considerable attention. Aumen (1995) provides a detailed account of the natural and management history of the lake. Smith and Collopy (1995) discuss the history of wading bird nesting at the lake during the study, and David (1994a) discusses nesting population trends during the 12 years prior to this study. Zaffke (1984), David (1994b), and Smith et al. (1995) review the population dynamics of foraging wading birds at the lake, and Smith (1995) discusses other aspects of the foraging habits of nesting adults.

A large, earthen dike nearly surrounds the lake and forms a sharp boundary between relatively natural emergent-marsh (400 km^2 coverage) and open-water habitats inside the dike and a diverse array of natural and artificial wetland habitats outside the dike. All the data considered herein are of birds from colonies located within the diked boundaries of the lake (Fig. 1), but many of the foraging flights led to habitats outside the diked area (Smith 1995). The emergent marsh habitats on the lake used most regularly by foraging wading birds include moderate-stature, wet-prairie assemblages featuring *Eleocharis, Rhynchospora, Panicum, Nymphaea, Polygonum,* and sparse *Typha* (Zaffke 1984, Smith et al. 1995). Prey sampling in such habitats generally revealed moderate densities of prey, but often a high diversity of both invertebrate and vertebrate prey species (Bull et al. 1992; McIvor and Smith 1992; Chick and McIvor, in press; Smith, unpubl. data). At low lake stages, exposed beds of submerged vegetation such as *Hydrilla, Vallisneria,* and *Potamogeton*—often mixed with the emergent *Nelumbo iutea*—harbored very high densities of forage fishes and grass shrimp (*Palaemonetes paludosus*) and attracted large numbers of foraging birds (Smith et al. 1995). The primary nest substrate is willow (*Salix caroliniana*). Habitats outside the dike that are regularly used by foraging birds include the floodplains of Fisheating Creek, Nicodemus Slough, and the Kissimmee River; isolated "pocket" and slough wetlands interspersed with cattle pastures to the north and west; agricultural field ditches to the southwest; and residential ditch, pond, and canal habitats in several areas (Fig. 1; Zaffke 1984; David 1994b; Smith, in press, unpubl. data). Very little is known about prey populations in these habitats.

Field methods.—Each year from 1989–1992, I followed individual and small groups of unmarked adult birds from nesting colonies to foraging grounds in a Cessna 172 fixed-wing aircraft. Each season, I began following birds once eggs started to hatch and continued flights until most nestlings had fledged. I concentrated on large, mixed-species colonies in which I conducted concurrent nesting success studies (Smith and Collopy 1995), but I also periodically followed birds from other colonies. I followed birds every week and each week I tried to follow some individuals of each of the four study species from each of the focal colonies. Up to five other ciconiiform species nested in the colonies (Smith and Collopy 1995), but I did not collect following-flight data for them. I conducted surveys throughout the day, as long as activity levels were sufficient to ensure a consistent source of birds to follow.

I began each following-flight by circling above the chosen colony at an altitude greater than 150 m, and generally followed the first bird or closely associated, conspecific group of birds to depart. I then monitored the progress of the bird(s) by flying in slow, wide circles around and above it at horizontal and vertical distances sufficient to avoid disturbing its flight (always distances >150 m, usually much greater for white species). I followed each

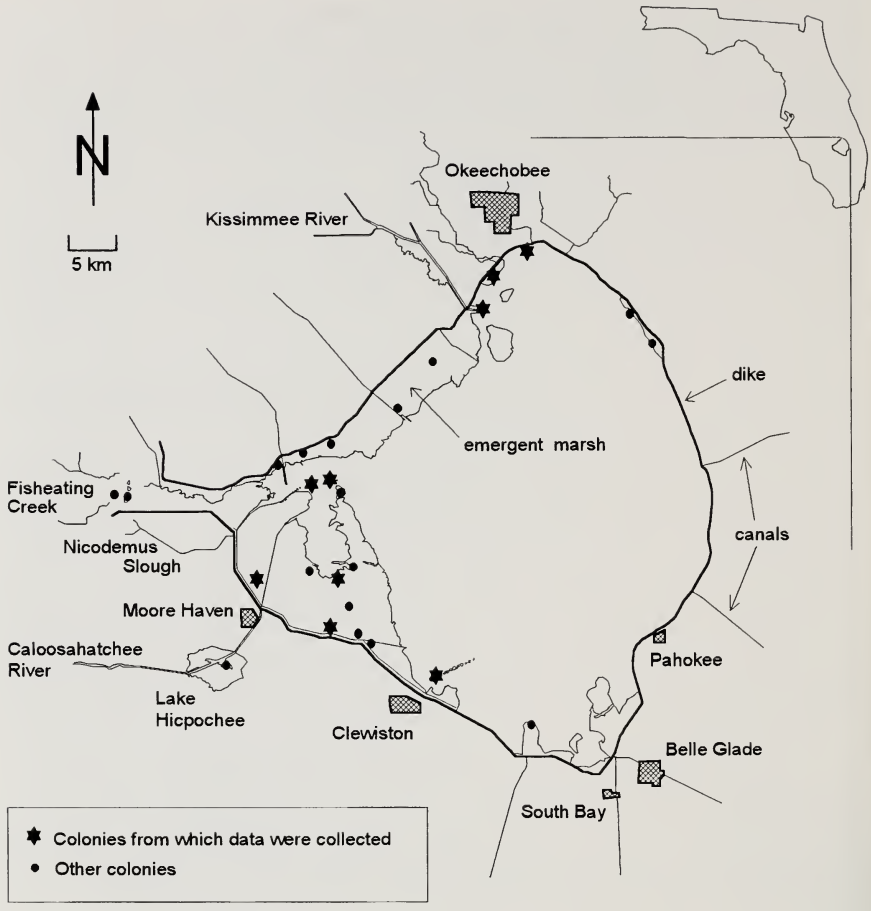

FIG. 1. A geographic overview of the Lake Okeechobee area showing the locations of nesting colonies used by the four study species.

bird until it landed in an area where foraging was possible and remained long enough that I could record an endpoint coordinate, a stop time, a description of the chosen habitat, and the flock joined, and I could take a photograph of the area. Recording these data usually took 2–3 min; if the bird began moving again before I finished, I continued the flight. The only time I deviated from this protocol was when I had followed a group of birds that did not all land in the same location. In this case, I attempted to document the first landing spot for all birds, but was unable to record the final details for each until the last bird had landed and I could return to previous landing spots to record additional data. Sometimes I was forced to abandon individuals that ultimately followed widely divergent paths. In these cases, I continued to follow the larger of the split groups or arbitrarily chose one of a split pair to finish following.

Analytical methods.—A primary assumption behind most parametric statistical tests is that the observations to be analyzed are independent of one another; i.e., the value of or random error associated with a given observation is not related to other such values in any systematic way (e.g., see Sokal and Rohlf 1981:401–402). The foraging habitat choices of birds that traveled in groups may have depended on the results of social interaction. If so, the individual-bird observations in each set would be interdependent, and one should analyze each group of observations as a single record. However, it is also possible that groups formed simply because several birds happened to depart for a known foraging location at the same time (sensu Bayer 1982). Thus, eliminating all apparently redundant group observations may unnecessarily sacrifice valid data. Accordingly, I ran the analyses discussed below twice, once with all individual-bird observations included and once with each set of group observations considered as a single observation. In all such cases, I found that although there were subtle differences in significance levels, there were no marked differences in the conclusions suggested. Therefore, the analyses I present below all represent datasets with each bird considered an independent unit.

I conducted a likelihood ratio Chi-square (χ^2) test of independence (Sokal and Rohlf 1981: 735–738; performed in SAS, SAS Institute, Inc. 1988) and χ^2 multiple comparisons (Fleiss 1981:140–141) to elucidate whether species differed in their tendency to travel in groups from colonies to foraging sites. I used a standard least-squares analysis of variance (ANOVA) with Bonferroni *t*-test multiple comparisons to determine whether species differed with regard to the size of the groups in which they traveled (performed in SYSTAT, Wilkinson 1990). I log-transformed ($\ln[x]$) the group-size data to normalize residuals.

I conducted a likelihood ratio χ^2 test of independence to determine whether species differed in their tendencies to land alone, near others, or in the immediate vicinity of other birds at foraging sites. A bird that landed alone landed in a habitat patch devoid of other birds; i.e., the presence of other birds could not have affected the birds' choice of the particular foraging spot (no birds in similar habitat within distances on the order of hundreds of meters). A bird that landed near others landed in a habitat patch where one or more other birds were already foraging but did not join a concentrated flock or land in the immediate vicinity of another bird. Estimating distances from the air is difficult, so the definition of what qualified as near was imprecise. Essentially, I classified a bird as having landed in the immediate vicinity of others if its foraging movements were likely to intersect those of other birds (inter-bird distances on the order of <10 m, usually 1–3 m). In contrast, I classified a bird as having landed only near others if the presence of other birds foraging nearby in the same habitat may have influenced the bird's selection, but it was unlikely the bird would cross paths with the other birds (inter-bird distances on the order of tens of meters).

I conducted a separate likelihood ratio χ^2 test of independence with χ^2 multiple comparisons to determine whether species differed in their tendency to join conspecifics at foraging sites. I limited the data to followed birds that landed near or in the immediate vicinity of others. I also conducted an ANOVA with Bonferroni *t*-test multiple comparisons to determine whether species differed with regard to the size of the feeding flocks each joined. Again, I limited the data to birds that landed near or in the immediate vicinity of others. I calculated flock sizes as the total of all birds considered near or in the immediate vicinity of the followed bird. I log-transformed ($\ln[x]$) the flock size data to normalize residuals.

RESULTS

Great Egrets were least likely among the species studied to travel to foraging sites in groups; only 9% of the birds followed departed the colonies with one or more traveling companions (Table 1). Tricolored

TABLE 1

CHI-SQUARE TESTS EXAMINING SPECIES' TENDENCIES TO TRAVEL IN GROUPS TO FORAGING LOCATIONS

Species	Total birds departed	Total birds followed to landing	Total birds departed in groups[a]	Mean group size[b]	Maximum group size	% Groups dispersed before landing	% Groups partially dispersed before landing
Great Egret	357	356	32 (9)	2.2 ± 0.79 (14)	4	29	0
Snowy Egret	242	237	64 (26)	2.3 ± 1.08 (27)	4	41	0
Tricolored Heron	84	81	16 (19)	2.5 ± 1.18 (6)	5	83	0
White Ibis	324	286	208 (64)	3.0 ± 1.05 (62)	11	31	19

[a] Likelihood ratio $\chi^2 = 259.6$, df = 3, $P < 0.001$; χ^2 multiple comparisons with experiment-wise $\alpha = 0.05$—White Ibises significantly more likely than others to depart in groups; Great Egrets significantly more likely to depart alone. Values in parentheses indicate percent of total.

[b] ANOVA: $F = 3.75$, df = 3, 105, $P = 0.013$; Bonferroni *t*-test multiple comparisons with experiment-wise $\alpha = 0.05$—White Ibis groups significantly larger than Snowy Egret groups (difference between White Ibises and Great Egrets significant if experiment-wise $\alpha = 0.10$). Birds that traveled alone were excluded from this analysis. The means and standard errors given represent back-transformed least squares estimates. The lower numbers in parentheses indicate group sample sizes.

Herons and Snowy Egrets were significantly more likely than Great Egrets to depart in groups (19% and 26% of all birds, respectively), but only among White Ibises did a majority leave in groups (64% of all birds; Table 1). Moreover, when White Ibises traveled in groups, they tended to travel in larger groups than other species. The only significant difference with the experiment-wise $\alpha = 0.05$ was the comparison of White Ibises and Snowy Egrets (Table 1). However, Great Egret groups averaged smaller than Snowy Egret groups, but due to a smaller sample size, the difference relative to White Ibises was significant only if the experiment-wise α was relaxed to 0.10. Snowy Egrets and Tricolored Herons were significantly more likely than Great Egrets to depart in groups; however, more of the Snowy Egret and especially Tricolored Heron groups dispersed before landing (Table 1). As a result, only 2% of the Tricolored Herons landed with a traveling companion, compared to 7% of the Great Egrets and 15% of the Snowy Egrets. Half of the White Ibis groups also dispersed to some degree before landing, but still 41% of the individual ibises landed with one or more of their original traveling companions.

A majority of individuals of all species landed either with or near other foraging birds (Table 2). White Ibises were the most likely to land in the immediate vicinity of other birds, and rarely landed in areas devoid of

TABLE 2

CHI-SQUARE TESTS EXAMINING SPECIES' TENDENCIES TO JOIN OTHER BIRDS AT FORAGING SITES, AND AN ANOVA EXAMINING SPECIES' DIFFERENCES WITH REGARDS TO THE SIZE OF THE FEEDING FLOCKS EACH TENDED TO JOIN

Species	Total birds followed[a]	Landed alone[a]	Landed near others[a]	Landed with flock[a]	% Joining birds that landed near or with conspecifics[b]	Mean size of feeding flock joined[c]
Great Egret	356	102/66* (29)	59/51 (16)	195/239* (55)	87	11.7 ± 2.46 (1–650)
Snowy Egret	237	22/44* (9)	38/34 (16)	177/159 (75)	96	15.7 ± 1.13 (1–955)
Tricolored Heron	82	35/15* (43)	16/12 (20)	30/54* (37)	54	5.2 ± 1.29 (1–100)
White Ibis	286	19/53* (7)	25/41* (9)	242/192* (84)	97	30.9 ± 1.11 (1–735)

[a] Likelihood ratio χ^2 test of species-specific proportions: $\chi = 124.6$, df = 6, $P < 0.001$, indicating that species differed in their tendency to join other birds at foraging sites. Values for each species and category: observed/expected counts (asterisks indicate significant [$P \leq 0.05$] difference between observed and expected frequencies), with percentage of observed counts below in parentheses.

[b] Likelihood ratio χ^2 test of species-specific proportions: $\chi^2 = 74.0$, df = 3, $P < 0.001$; χ^2 multiple comparisons with experiment-wise $\alpha = 0.05$—Great Egrets and especially Tricolored Herons significantly less likely than other species to join conspecifics.

[c] ANOVA: $F = 63.9$, df = 3, 777, $P < 0.001$; Bonferroni t-test multiple comparisons with experiment-wise $\alpha = 0.05$—White Ibises joined significantly larger flocks than all other species, and Snowy Egrets and Great Egrets joined significantly larger flocks than Tricolored Herons. Values for each species: back-transformed least squares means and standard errors, with the range of observed flock sizes given below in parentheses.

other birds. Moreover, ibises that joined groups joined significantly larger groups than other species (Table 2). Snowy Egrets also usually joined or at least landed near other birds. Great Egrets were less likely to land in the immediate vicinity of other birds but still usually landed at least near other birds rather than alone. Tricolored Herons were more likely to land alone than in the immediate vicinity of other birds but usually chose habitats already occupied by one or more birds. Great Egrets and Snowy Egrets joined significantly smaller groups than did White Ibises but significantly larger groups than Tricolored Herons (Table 2).

Tricolored Herons that joined other birds at foraging sites were significantly less likely than other species to join conspecifics or flocks that included conspecifics (Table 2), having done so only slightly more than half the time (54%). Great Egrets were also significantly less likely than Snowy Egrets and White Ibises to join conspecifics, but 87% of the joining birds did so. In addition, 37–43% of the Snowy Egrets, White Ibises, and Great Egrets that landed with other birds either joined or landed near only conspecific individuals, whereas the proportion dropped to only 17% for Tricolored Herons. Great Egrets and Tricolored Herons that joined

mixed-species flocks joined flocks that included Snowy Egrets (73 and 63% of the birds, respectively) more often than flocks that included White Ibises (54 and 29%). Snowy Egrets and White Ibises usually joined flocks that included conspecifics, but White Ibises joined flocks that included Snowy Egrets (67% of the birds that joined mixed flocks) more often than Snowy Egrets joined flocks that included White Ibises (50%).

DISCUSSION

My findings concerning each species' propensity to travel in groups were generally consistent with those of previous studies. Custer and Osborn (1978) found that White Ibises in North Carolina traveled with conspecifics on 17% of the monitored flights, whereas only 3–5% of the Snowy Egret, Tricolored Heron, and Great Egret flights involved more than one individual. Ogden (1978) noted that 29% of the Snowy Egrets and 15% of the Tricolored Herons that departed from a colony in the Everglades did so in groups. Maccarone and Parsons (1988) monitored foraging flights from two colonies off Staten Island, New York, and found that 7% of the Snowy Egret flights and 3% of the Great Egret flights involved groups of two or three birds. Erwin (1983) found that only 2–4% of the Snowy Egrets, Tricolored Herons, and Great Egrets departed in groups (2–3 birds) from the colony he studied in North Carolina. Even fewer Snowy Egrets and Tricolored Herons departed in groups from the colony he studied in Virginia (Erwin 1984). Frederick and Collopy (1988) indicated that most of the Great Egrets, Snowy Egrets, and White Ibises they followed from colonies in the Everglades were solitary travelers but that the ibises occasionally departed in groups. Thus, the data consistently indicate that White Ibises are the most likely to travel in groups and that Snowy Egrets are slightly more likely to do so than Great Egrets and Tricolored Herons.

The stronger tendency for ibises to travel in groups might suggest greater reliance on information exchange at the colony to ensure profitable foraging opportunities. Alternatively, Bayer's (1982) hypothesis may apply; i.e., group departures are a statistical artifact of grouped arrivals. Any tendency to travel in groups may simply be indicative of temporally consistent use of established flight lines to common foraging grounds (Erwin 1983). In general, the preponderance of solitary travelers observed during this and the other studies cited above suggests that information exchange at colonies is not a particularly important determinant of wading bird foraging success (J. C. Ogden, pers. comm.). Moreover, the nature of a species' foraging strategy may be a primary determinant of social tendencies. For instance, because ibises typically forage using a tactile, grope-foraging technique, they increase the efficiency of their foraging

primarily through habitat selection, rather than by actively searching for concentrations of prey (Kushlan 1979). Flocking and group feeding help insure that foraging time is spent in relatively profitable patches of habitat and reduces the time spent searching for such patches (Ward and Zahavi 1973, Krebs 1974, Kushlan 1979). In addition, the "beater" effect of foraging around other birds (Kushlan 1979) may increase the chance of random encounters with moving prey and, therefore, may be of particular benefit to tactile-feeding species like ibises. Traveling in groups from colonies may simply be one mechanism for insuring that foraging partners are available for interaction and may also facilitate location of productive habitat via local enhancement (Evans 1982, Erwin 1983). Other data provide additional support for this hypothesis. Among the species studied, White Ibises were the most likely to join other foraging birds at foraging sites, usually landed in the immediate vicinity of other birds as opposed to only nearby, and tended to join larger flocks than other species.

Traveling in groups may not have been common, but the majority of individuals of all species did choose to land with or near other wading birds at foraging sites. This fact suggests that all species frequently relied on local enhancement to identify at least quality foraging regions, if not specific prey-rich habitat patches (Krebs 1974, Kushlan 1977, Caldwell 1981, Erwin 1983, Master 1992). Again, however, differences in foraging strategies may also have influenced species' tendencies toward aggregation. For instance, Tricolored Herons were the least inclined to join concentrated feeding flocks and usually landed near smaller groups than other species. These results are consistent with previous studies that showed Tricolored Herons usually remain on the periphery of mixed-species aggregations (Willard 1977, Kushlan 1978b, Master 1992), are more often found in smaller groups (Kushlan 1976a, Erwin 1983) or less often in association with feeding flocks than other species (Willard 1977), and do not necessarily increase their foraging efficiency by associating with aggregations (Master et al. 1993, but see Caldwell 1981). Tricolored Herons often feed solitarily using either active disturb-and-chase or stealth techniques, depending on the habitat (Meyerricks 1962; Jenni 1969; Willard 1977; Murdich 1978; Rodgers 1983; Kent 1986; Smith, unpubl. data). The efficiency of both techniques is probably less effective near dense aggregations (Kushlan 1978b). Thus, the species' strategy is best-suited to non-aggregation foraging, but choosing sites near other foraging birds—i.e., at least in similar habitat—might increase the probability of finding rich prey resources.

Tricolored Herons routinely achieve high levels of reproductive success compared to other ciconiiforms (e.g., Frederick and Collopy 1988, Bancroft et al. 1990, Smith and Collopy 1995). This fact suggests that their

solitary foraging strategy is productive, which in turn suggests that accruing benefits from local enhancement and information exchange at nesting colonies is not a crucial prerequisite for successful nesting in the region. However, it was noteworthy that Tricolored Herons were the only species for which I discovered significant negative associations between mean flight distances and colony-specific estimates of nest success and productivity (Smith 1995).

Master et al. (1993) found that, although Great Egrets expended less energy when foraging in association with mixed-species flocks, they did not increase foraging efficiency (but see Caldwell 1981). In contrast, Wiggins (1991) found that Great Egrets feeding in monospecific groups were less likely to expend energy chasing other birds and achieved higher capture rates and efficiency. The biomass intake rate of solitary birds was equivalent because they usually took larger fish, but solitary birds were more likely to expend considerable energy defending their feeding territory. He concluded that Great Egrets in Texas probably aggregate only when small fishes are sufficiently concentrated that a high rate of capture yields a similar or greater level of energy gain than fewer captures of larger fish. Erwin (1983) found that Great Egrets were not common in large groups, further indicating that the species often prefers to feed in smaller groups or solitarily. Such situations are probably more amenable to use of the species' usual foraging mode, a slow-stalking approach (Willard 1977, Kushlan 1978b, Hom 1983, Rodgers 1983, McIvor and Smith 1992).

My observations suggested that Great Egrets were most likely to congregate in large, dense groups (up to several hundred individuals) when foraging in relatively open, moderate-depth water in between or on the fringes of beds of submerged vegetation (unpubl. data). At these times, the most frequently captured prey were moderate-sized sunfish and bass (Centrarchidae), schooling fishes such as shad (*Dorosoma* sp.), and golden shiners (*Notemigonus crysoleucas*). Great Blue Herons (*Ardea herodias*) and Wood Storks (*Mycteria americana*) were common members of these aggregations. My observations of many such flocks (see McIvor and Smith 1992) suggested that the dense concentration of birds elicited chaotic movements among the fishes that rendered them more susceptible to capture. The occurrence of such large groups was probably dependent on the fact that the fish had become concentrated by a severe drought (Smith et al. 1995). Otherwise, although I frequently observed Great Egrets feeding with mixed-species flocks in a variety of situations, I more commonly observed scattered individuals in wet-prairie habitats dominated by *Eleocharis* or *Panicum* (Smith et al. 1995). In addition, nesting Great Egrets were unusual because, especially during drought periods,

they took advantage of a unique, relatively asocial foraging opportunity–panhandling fish scraps at residential cleaning stations (Smith 1995).

Snowy Egrets were less prone to travel in groups, but like White Ibises, they usually joined other birds at foraging sites. Snowy Egrets have frequently been cited as the primary attractor and a core species in mixed-species aggregations (Willard 1977, Caldwell 1981, Erwin 1983, Master 1992). Jenni (1969) also noted that Snowy Egrets tended to be more social than Tricolored Herons. Master et al. (1993) suggested that Snowy Egrets may be obligate aggregation foragers, because gains in foraging efficiency derived from aggregation foraging (Caldwell 1981, Master et al. 1993) may be essential to meet the species' more stringent daily energy requirements (Kent 1986). Itzkowitz (1984) regularly observed transient, solitarily foraging Snowy Egrets at Stone Harbor, New Jersey, but his observations usually occurred after early-morning aggregations had dispersed (Master 1992 and pers. comm.). I also regularly observed solitary Snowy Egrets foraging at Lake Okeechobee. A common example involved the use of energetically expensive, aerial foraging methods to exploit surface concentrations of small fishes in deep-water *Hydrilla* habitats (McIvor and Smith 1992, Smith et al. 1995), which suggests that energy constraints may not have been a critical issue for the adult birds (also see Edelson and Collopy 1990). Snowy Egrets also are well known for their use of foot-stirring as a disturbance technique, a strategy most suited to solitary foraging (Meyerriecks 1962, Willard 1977, Hom 1983, Rodgers 1983, Master et al. 1992). These observations confirm that Snowy Egrets employ a diverse array of aggregation and solitary foraging strategies (also see Kushlan 1978b), but, nonetheless, at Lake Okeechobee, I observed far more birds in aggregations than alone (Table 2, but also confirmed by systematic, lakewide surveys [Smith et al. 1995] of foraging birds; Smith, unpubl. data).

Tricolored Herons that chose foraging sites with other birds present were more likely to choose areas occupied by white-plumaged species than those occupied by only conspecifics and were more likely to associate with Snowy Egrets than with White Ibises or Great Egrets. This is consistent with Caldwell's (1981) finding that the species was preferentially attracted to monospecific flocks of model Snowy Egrets as opposed to Great Egret or mixed-species flocks. However, Great Egrets in this study joined only other Great Egrets 37% of the time, which differs from Caldwell's (1981) findings that the species was preferentially attracted to monospecific flocks of model Snowy Egrets but never to monospecific flocks of Great Egrets. Nonetheless, during my study, Great Egrets that did join non-conspecific individuals joined Snowy Egrets more often than

other species. In addition, White Ibises joined flocks that included Snowy Egrets more often than flocks that included White Ibises.

I did not gather information about the relative availability of flocks of different composition over the entire study area, so I cannot be sure that the indicated trends reflect preferences. However, White Ibises were generally the most abundant species observed in the region, followed by Great Egrets, and then Snowy Egrets (Smith et al. 1995). Thus, the results seem to lend support for the hypothesis that Snowy Egrets, in particular, act as an attractor for other species. White plumage undoubtedly plays a role in this association (Armstrong 1970, Kushlan 1977). Kushlan (1978a) showed that White Ibises sometimes act as an attractor for other species in the Everglades. However, there must be additional factors at work, since Snowy Egrets are commonly singled-out as an attractor species. Caldwell (1981) suggested that Snowy Egrets are prime indicators of high-quality foraging habitat because their high visual acuity facilitates prey location and their high position in the interspecific dominance hierarchy enables them to usurp prime feeding sites from other similar-sized species. Another possibility is that flocks of Snowy Egrets may be indicative of certain types or concentrations of universally attractive prey. Great Egrets often focus on larger fishes and feed in water too deep for the smaller species, but they also regularly exploit smaller fishes, especially when feeding in association with mixed-species flocks (Willard 1977; Custer and Osbom 1978; Hom 1983; Bancroft et al. 1990; Smith, unpubl. data). White Ibises typically select less-active and cryptic crayfish (*Procambarus* sp.) and other benthic invertebrates—many of which are less-digestible and nutritionally inferior to fish—but often switch to fish when they are highly concentrated (Kushlan and Kushlan 1975; Kushlan 1976b, 1979). In contrast, Snowy Egrets usually aggregate to feed on concentrations of small, schooling fishes (e.g., mosquitofish, *Gambusia holbrooki*, or sailfin mollies, *Poecilia latipinna*, in freshwater marshes of southern Florida) or relatively visible and moderate-sized crustaceans such as grass shrimp (Jenni 1969; Kent 1986; Bancroft et al. 1990; McIvor and Smith 1992; Smith, unpubl. data). Thus, flocks of Snowy Egrets may guarantee the presence of prey species that most wading bird species (including Tricolored Herons) will exploit when available, whereas aggregations of other species may not provide such a guarantee for non-conspecific individuals.

ACKNOWLEDGMENTS

This manuscript represents a redraft of a portion of the author's Ph.D. dissertation completed at the University of Florida in 1994. Funding for this work was provided by the South Florida Water Management District, West Palm Beach, Florida. Flight services were

provided by James Wyatt Enterprises of Homestead, Florida, and American Aviation, Inc. of Pompano Beach, Florida. Michael Plotkin, Chris Goguen, and Ruthe Smith assisted with data processing. Constructive reviews of earlier drafts by Michael W. Collopy, Peter C. Frederick, Carole C. McIvor, Malcolm C. Coulter, Terry L. Master, and John C. Ogden improved the quality of the manuscript.

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Wilson Bull., 107(3), 1995, pp. 452–462

DISTRIBUTION AND ABUNDANCE OF RAPTORS IN PUERTO RICO

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Abstract.—From July 1986 to June 1988, I counted all raptors (Falconiformes and Strigiformes) seen or heard along 15 8-km routes in the three major life zones of Puerto Rico (moist, wet, and dry). Red-tailed Hawks (*Buteo jamaicensis*) and American Kestrels (*Falco sparverius*) were the most abundant year-round residents. Red-tailed Hawks were more abundant in the moist zone than in the wet zone. American Kestrels did not differ significantly in the dry and moist zones. Red-tailed Hawks were more abundant than American Kestrels in the moist zone. The most abundant winter residents were Merlins (*F. columbarius*), Peregrine Falcons (*F. peregrinus,*) and Ospreys (*Pandion haliaetus*); all three species were frequently detected in the dry zone but were less abundant than American Kestrels. The abundances of Merlins, Peregrine Falcons, and Ospreys did not differ significantly. The abundances of raptors (pooled) peaked in autumn (September–November) and winter (December–February). Roadside counts were highly variable (coefficients of variation ranged from 85–243%). As a result, the within-year sample-sizes (8-km routes) needed to provide confidence limits of $\pm$10–50% ($t_{0.05} \approx 2.0$) on mean abundance estimates ($\bar{Y}$) of the most abundant species in the life zones were high. *Received 19 Oct. 1994, accepted 15 Feb. 1995.*

Eight diurnal raptors are reported for Puerto Rico: Sharp-shinned Hawk (*Accipiter striatus*), Red-tailed Hawk (*Buteo jamaicensis*), Broad-winged Hawk (*B. platypterus*), Northern Harrier (*Circus cyaneus*), Osprey (*Pandion haliaetus*), Peregrine Falcon (*Falco peregrinus*), Merlin (*F. columbarius*), and American Kestrel (*F. sparverius*); and two species of owls, Puerto Rican Screech-Owl (*Otus nudipes*) and Short-eared Owl (*Asio flammeus*). Northern Harriers, Peregrine Falcons, Merlins, and Ospreys are winter residents. Sharp-shinned Hawks, Red-tailed Hawks, Broad-winged Hawks, American Kestrels, Puerto Rican Screech-Owls, and Short-eared Owls are year-round residents (Biaggi 1983, Raffaele 1989). General information about the diurnal and nocturnal raptors of Puerto Rico can be found in Pérez-Rivera and Cotté-Santana (1977), Biaggi (1983), Wiley (1985), and Raffaele (1989). Detailed studies have been conducted by Santana et al. (1986) and Delannoy and Cruz (1988). Little is known, however, about the distribution and abundance patterns of raptors in Puerto Rico. From July 1986 to June 1988, I counted raptors in the same sampling units used to study the distribution and abundance of pigeons and doves (Columbidae) in Puerto Rico (Rivera-Milán 1990, 1992, 1993). My main objectives were to examine seasonal distribution and abundance patterns of raptors and to determine the number of within-

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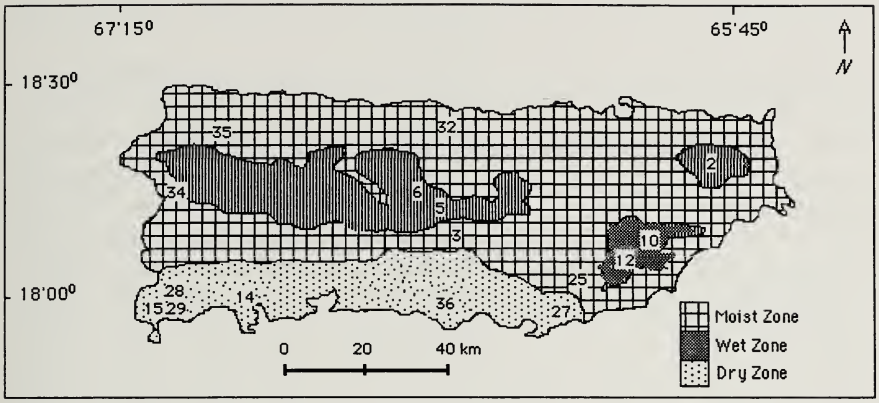


FIG. 1. Map showing the 8-km routes sampled in the three major life zones of Puerto Rico.

year sampling units (8-km routes) needed to have ±10–50% ($t_{0.05} \approx 2.0$) in the relative precision of mean estimates ($\bar{Y}$) of the most abundant resident species in the three major life zones of Puerto Rico.

STUDY AREAS AND METHODS

Puerto Rico is the easternmost and smallest of the Greater Antilles (17°55′–18°35′ north, 65°37′–67°17′ west; land area is about 8903 km²). The three major life zones of the island are the subtropical moist zone (≈5326 km²), the subtropical wet zone (2124 km²), and the subtropical dry zone (1216 km²; Fig. 1). The forest area of Puerto Rico, which covers approximately 3400 km² (38%) of the island, is dominated by second-growth forests in lower and upper montane habitats (Ewel and Whitmore 1973, Little et al. 1977, Birdsey and Weaver 1982, Silander et al. 1986, Ortiz 1989).

From July 1986 to June 1988, 15 8-km routes were sampled once per month in the three major life zones of the Puerto Rican mainland (five routes/life zone; Fig. 1). Each route had six stations spaced at 1.6-km (1-mi) intervals. At each station, I stopped for three minutes and counted all the raptors seen or heard. The driving speed between stations fluctuated between 16 and 32 kph, depending upon the terrain and traffic conditions. The counts started at 05:30 and finished at 10:30 h, but were discontinued if it rained or if wind speed exceeded 19 kph. A separate record was kept of the individuals of each species seen while driving between the 3-min stations. Detailed information about the routes sampled can be found in Rivera-Milán (1990, 1992, 1993).

Call- and sight-counts were used to generate descriptive statistics. The within-year sample-sizes (8-km routes) needed to provide 95% confidence limits for an estimate of mean abundance ($\bar{Y}$) were calculated according to Eberhardt (1978:229–230). Samples sizes were estimated for confidence limits ranging from 10–50% of the true mean for Red-tailed Hawks and American Kestrels in each life zone. Analysis of variance (ANOVA) with repeated measures at one factor (season) was used to examine abundance patterns of Red-tailed Hawks and American Kestrels in the life zones (Winer 1971; Gurevitch and Chester 1986; Beal and Khamis 1990, 1991; Quinn and Keough 1991). Separate ANOVAs were conducted for each species. A one-tailed unpaired *t*-test was used to compare mean abundance estimates

Table 1

Descriptive Statistics of Roadside Counts of Raptors on the Puerto Rican Mainland

Species	Life zone	Mean	SE	CV (%)	Sum	N
Red-tailed Hawk	Moist zone	5.87	1.09	91	141	24
Red-tailed Hawk	Wet zone	2.29	0.40	86	55	24
American Kestrel	Dry zone	2.67	0.55	101	64	24
American Kestrel	Moist zone	1.71	0.30	85	41	24
Puerto Rican Screech Owl	Moist-wet zone	1.45	0.30	172	24	24
Merlin	Dry-moist zone	0.54	0.23	204	13	24
Peregrine Falcon	Dry-moist zone	0.50	0.17	167	12	24
Osprey	Dry zone	0.50	0.18	177	11	24
Broad-winged Hawk	Wet zone	0.46	0.19	203	11	24
Puerto Rican Sharp-shinned Hawk	Wet zone	0.25	0.12	243	6	24

of Red-tailed Hawks in the moist and wet zones and mean abundance estimates of Kestrels in the moist and dry zones (intraspecific comparisons across life zones). A one-tailed unpaired *t*-test was also used to compare mean abundance estimates of Red-tailed Hawks and American Kestrels in the moist zone and mean abundance estimates of American Kestrels, Merlins, Peregrine Falcons, and Ospreys in the dry zone (interspecific comparisons within a life zone). Since means and standard deviations were positively correlated (Pearson's $r = 0.97$, df = 8, $P = 0.00001$), counts were log-transformed before conducting statistical analyses (Sokal and Rohlf 1981). Details of other statistical analyses are given with the corresponding results. Statistics were performed with the programs SuperANOVA and StatView II (Abacus Concepts, Inc., Berkeley, California, 1987, 1989). Significance was accepted at $P \leq 0.05$.

Table 2

Analysis of Variance with Repeated Measures at One Factor (Season) for Counts of Red-tailed Hawks in the Moist and Wet Zones of Puerto Rico

Source of variation	df	Sum of squares	Mean square	*F*-test	*P*-value
Life zone	1	3.801	3.801	5.279	0.051
Routes (life zone)	8	5.760	0.720		
Season	3	2.442	0.814	1.724	0.188
Life zone × season	3	2.055	0.685	1.451	0.276
Routes (life zone) × season	24	11.327	0.472		

Repeated measures:	Winter	Spring	Summer	Autumn
Life zone				
Moist	1.298	1.621	1.916	2.258
Wet	1.449	0.635	1.196	1.346

RESULTS

Red-tailed Hawks were more abundant in the moist zone than in the wet zone (t-statistic = 3.1, df = 46, P = 0.003; Tables 1 and 2). Their abundances increased from autumn (September–November) to winter (December–February) in the wet zone and from summer (June–August) to autumn in the moist zone (Table 2 and Fig. 2A). Red-tailed Hawks were relatively uncommon in the dry zone.

Abundance of American Kestrels did not differ significantly in the dry and moist zones (t = 1.2, df = 46, P = 0.252; Tables 1 and 3). They increased from autumn to winter in the dry zone and from summer to autumn in the moist zone (Table 3 and Fig. 2B). American Kestrels were relatively uncommon in the wet zone. Red-tailed Hawks were more abundant than American Kestrels in the moist zone (t = 3.7, df = 46, P = 0.001).

The Puerto Rican Screech-Owl was the third most abundant raptor in the moist and wet zones (Table 1 and Fig. 3A). Screech-Owl counts increased from autumn to winter in three 8-km routes sampled from July 1986 to June 1988 (Fig. 3A). They were not recorded in the sampling units of the dry zone.

The Broad-winged Hawk and Puerto Rican Sharp-shinned Hawk were the least abundant year-round residents (Table 1 and Fig. 3B). Eleven Broad-winged Hawks were found in the wet zone; six occurred in the Luquillo National Rainforest (route #2; Fig. 1). Six Sharp-shinned Hawks were in the wet zone; five occurred in the Carite State Forest, Cayey (routes #10 and #12; Fig. 1). Broad-winged Hawks and Sharp-shinned Hawks were not observed in the moist and dry zones.

The most common winter residents were Merlins, Peregrine Falcons, and Ospreys (Table 1 and Fig. 3C). Merlins and Peregrine Falcons were frequently found in agricultural areas and saltflats in the dry zone (routes #15 and #29; Fig. 1) but were less abundant than American Kestrels (t = 5.2, df = 46, $P < 0.001$; t = 5.1, df = 46, $P < 0.001$). Ospreys were also frequently detected in saltflats (routes #15 and #29; Fig. 1), but were less abundant than American Kestrels (t = 4.3, df = 46, $P < 0.001$). The rarest of the winter residents was the Northern Harrier. One Northern Harrier was found on the Cabo Rojo saltflats (route #15).

The Short-eared Owl was not found in the routes sampled, but was frequently flushed from the ground when conducting nest searches in the vicinity of route #15 (Rivera-Milán, unpubl. data). The Turkey Vulture (*Cathartes aura*) was not included in the roadside counts, but it was common in the agricultural areas of the dry zone (e.g., routes #15 and #29).

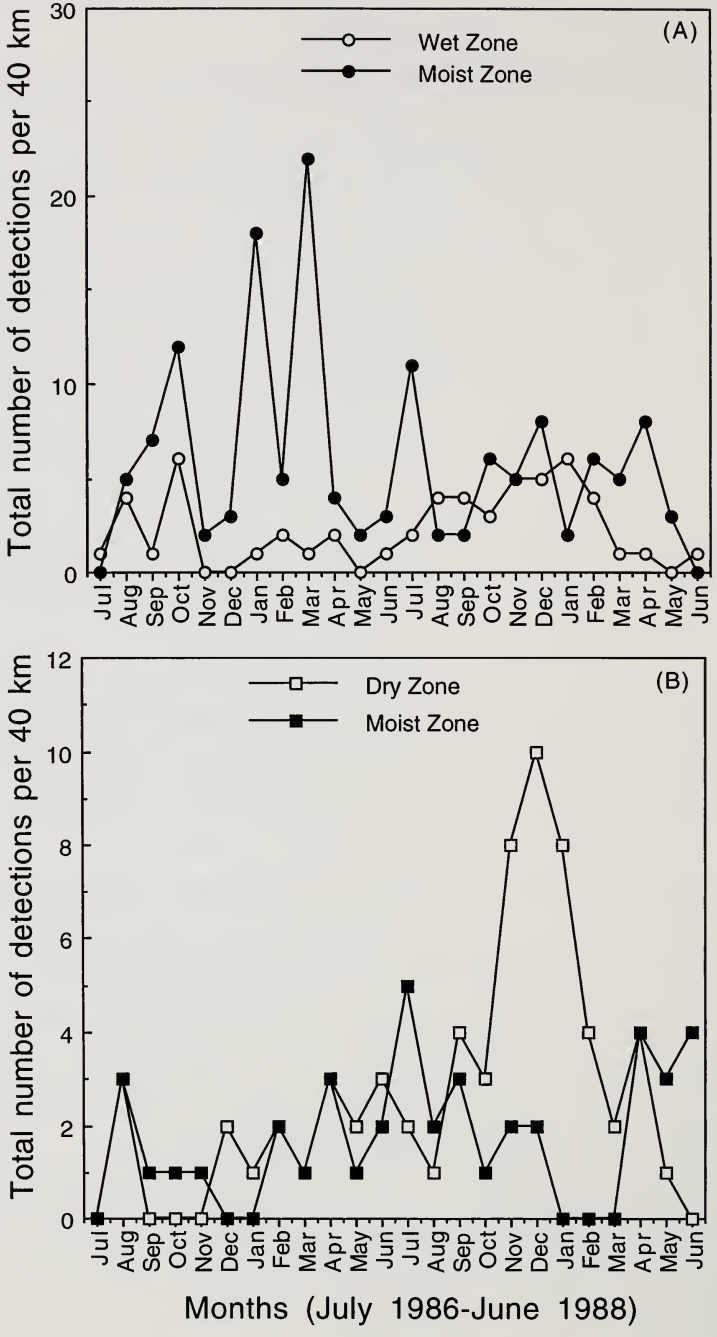

(A)
Wet Zone
Moist Zone
Total number of detections per 40 km
30
20
10
0
Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun
(B)
Dry Zone
Moist Zone
Total number of detections per 40 km
12
10
8
6
4
2
0
Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun
Months (July 1986-June 1988)

TABLE 3

ANALYSIS OF VARIANCE WITH REPEATED MEASURES AT ONE FACTOR (SEASON) FOR COUNTS OF AMERICAN KESTRELS IN THE MOIST AND DRY ZONES OF PUERTO RICO

Source of variation	df	Sum of squares	Mean square	*F*-test	*P*-value
Life zone	1	1.757	1.757	1.167	0.312[a]
Routes (life zone)	8	12.040	1.505		
Season	3	0.808	0.269	1.154	0.348
Life zone × season	3	1.618	0.539	2.309	0.102
Routes (life zone) × season	24	5.605	0.234		

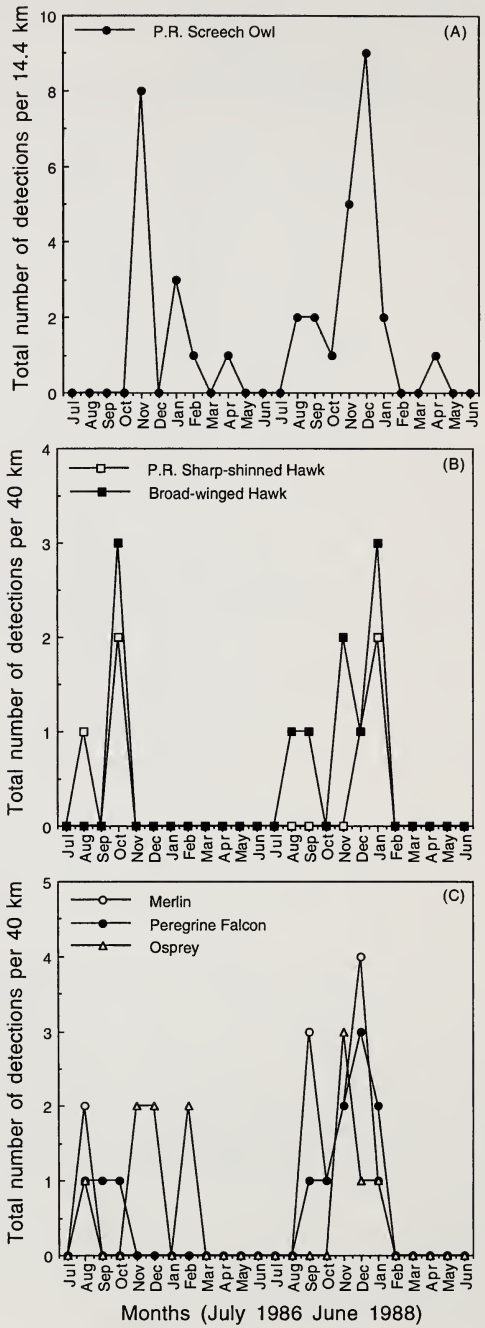
Repeated measures:	Winter	Spring	Summer	Autumn
Life zone				
Dry	1.522	1.230	1.125	1.590
Moist	0.520	0.851	1.259	1.160

The roadside counts of the most common year-round residents were highly variable, even on high-density routes. Annual coefficients of variation (CVs) of the counts of Red-tailed Hawks were in the order of 86-91% (24 counts in ten 8-km routes; Table 1 and Fig. 2A). Similarly, annual CVs of counts of American Kestrels were in the order of 85–101% (Table 1 and Fig. 2B). The counts of both species were positively-skewed and their variances were heterogeneous, but higher counts of Red-tailed Hawks were more extreme (positive) than higher counts of American Kestrels. Red-tailed Hawks were commonly detected soaring in groups of up to 11 birds; whereas American Kestrels usually were detected perching or flying singly or in pairs and had a more regular spatial distribution. The log-transformation normalized and stabilized the variances of the roadside counts.

Sample-size estimates varied by species, spatio-temporal scales, sensitivity (power of a test), and precision (width of a confidence interval). For example, at an α of 0.05 ($t_{0.05} \approx 2.0$) and a CV of 91%, 80 sampling units (8-km routes) were needed to provide confidence limits of $\pm 20\%$ on mean abundance estimates ($\bar{Y}$) of Red-tailed Hawks in the moist zone, and with a CV of 86%, 71 sampling units were needed in the wet zone (Fig. 4). With a CV of 85%, 69 sampling units were needed for American Kestrels in the moist zone; and with a CV of 101%, 98 sampling units

←

FIG. 2. Seasonal abundance patterns of Red-tailed Hawks (A) and American Kestrels (B) in Puerto Rico.


P.R. Screech Owl
(A)
Total number of detections per 14.4 km
P.R. Sharp-shinned Hawk
Broad-winged Hawk
(B)
Total number of detections per 40 km
Merlin
Peregrine Falcon
Osprey
(C)
Total number of detections per 40 km
Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun
Months (July 1986 June 1988)

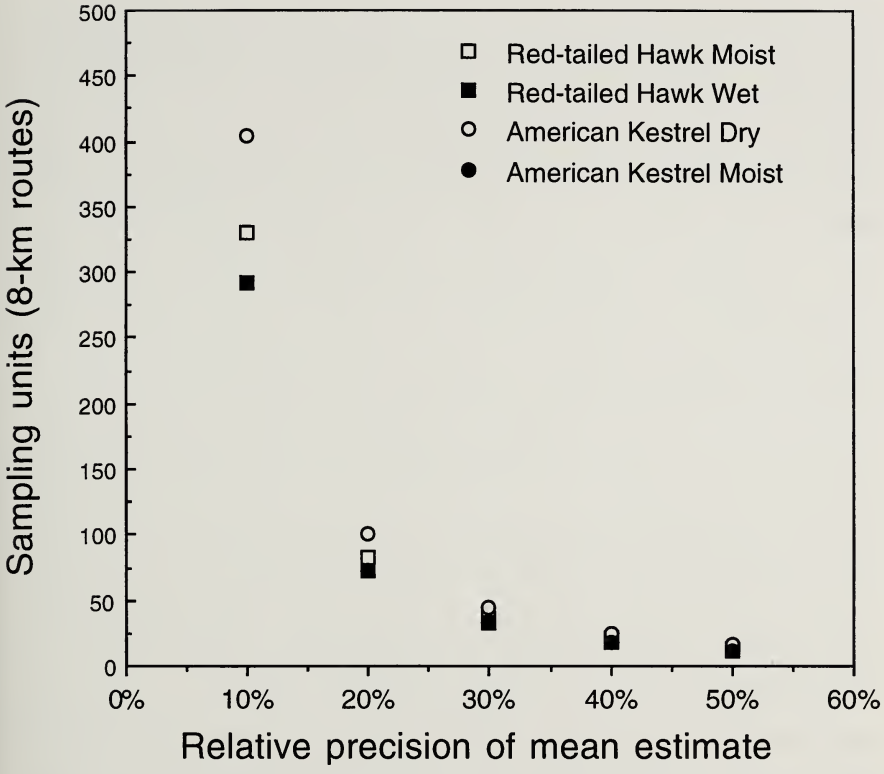


FIG. 4. Number of within-year sample-sizes (8-km routes) needed per life zone to provide confidence limits of ±10–50% ($t_{0.05} \approx 2.0$) on mean abundance estimates ($\bar{Y}$) of Red-tailed Hawks and American Kestrels.

were needed in the dry zone (Fig. 4). Sample-sizes decreased as a function of the desired precision of $\bar{Y}$.

DISCUSSION

The Red-tailed Hawk and American Kestrel were the most abundant year-round residents of Puerto Rico; and the Merlin, Peregrine Falcon, and Osprey were the most abundant winter residents. In general, the abundances of resident and migrant raptors (pooled) peaked from autumn to spring in Puerto Rico.

←

FIG. 3. Seasonal abundance patterns of Puerto Rican Screech-Owls (A), Broad-winged Hawks and Puerto Rican Sharp-shinned Hawks (B), and Merlins, Peregrine Falcons, and Ospreys (C).

The roadside counts of raptors were positively-skewed and their variances heterogeneous. Skewness and heterogeneity are characteristics of populations that are patchily-distributed in space and time because of habitat use and availability (Southwood 1978, Baker and Brooks 1981, Janes 1985, Preston 1990). Forest habitat loss and degradation and illegal hunting have been the major human-induced problems affecting the distribution and abundance of Sharp-shinned Hawks and Broad-winged Hawks in Puerto Rico (Pérez-Rivera and Cotté-Santana 1977, Wiley 1985, Santana et al. 1986, Delannoy and Cruz 1988). Although Sharp-shinned Hawks and Broad-winged Hawks seem to have suffered severe populations declines, mainly as a result of forest fragmentation, the populations of Red-tailed Hawks, American Kestrels, and Screech-Owls seem to have increased in edge habitats in suburban and agricultural landscapes (Wiley 1985). As human disturbance increases in lowland habitats of the moist zone, the abundance of Red-tailed Hawks may increase in montane habitats of the wet zone that are considered of critical importance for species such as Sharp-shinned Hawks, Broad-winged Hawks, and Puerto Rican Parrots (*Amazona vittata*), resulting in an increase of negative interactions (e.g., nestling predation, and competition for limited nest sites and foraging resources; Wiley 1985, Santana et al. 1986, Snyder et al. 1987, Delannoy and Cruz 1988, Lindsey et al. 1994).

The roadside counts were highly variable because of the distribution and abundance of raptors in the life zones. As a result, the within-year sample-sizes (8-km routes) needed to provide confidence limits of ±10-50% on $\bar{Y}$ were high. Presently, 30 8-km routes are sampled annually from the second week of May to the second week of June to monitor the population changes of Zenaida Doves (*Zenaida aurita*) and Scaly-naped Pigeons (*Columba squamosa*) in the three major life zones of Puerto Rico (Ramos et al. 1991), and it has been recommended that the number of routes be increased to 60 (30 in the moist zone, 20 in the wet zone, and 10 in the dry zone; Rivera-Milán 1993). This sampling scheme can be used to monitor annual population changes of widely-distributed and abundant species such as Red-tailed Hawks and American Kestrels inside and outside the forest reserves of Puerto Rico. According to the observed seasonal patterns of abundance, the best time of the year to sample raptor populations would be from August to December.

ACKNOWLEDGMENTS

G. Bonilla, M. Miranda, A. Ortiz, J. Pagán, D. Ramos, and E. Ramos provided field assistance. K. Beal, K. Bildstein, H. Raffaele, and J. Wiley reviewed earlier versions of the manuscript. The late J. Vivaldi provided support as Chief of the Terrestrial Ecology Section, Scientific Research Area, Puerto Rico Dept. of Natural Resources. Support was also provided

by the Marine and Estuarine Environmental Sciences Graduate Program and the Agricultural and Life Sciences Division of the Univ. of Maryland at College Park.

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Wilson Bull., 107(3), 1995, pp. 463–474

BIRD SPECIES RICHNESS IN RELATION TO ISOLATION OF ASPEN HABITATS

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Dean Urban,[3] and Dale Hein[2]

Abstract.—We studied 14 stands of aspen (*Populus tremuloides* Michx.) and their associated bird and plant communities in Rocky Mountain National Park, Colorado, in June 1993, to investigate the effects of habitat isolation on bird species richness. Selected aspen stands varied in their degree of isolation from other aspens, but were similar in area, elevation, and vegetation structure. The degree of isolation of aspen stands was expressed in four ways (1) distance to nearest neighboring aspen stand, (2) area-weighted distance to nearest neighboring aspen stand, (3) area-weighted distances of all aspen stands within 1500 m, and (4) total area of aspen stands within 1500 m. Isolation had no significant effect on the bird species richness of the 14 aspen stands studied. Regressions that incorporated isolation and vegetation parameters selected one-variable models, with percent shrub cover (0.5–2.0 m height) accounting for 58% of the variation in bird species richness ($r = 0.76$). Abundant understory vegetation in aspen stands may provide additional cover, food, and breeding habitat to support a larger number of bird species. *Received 8 Mar. 1994, accepted 1 Feb. 1995.*

Aspen (*Populus tremuloides* Michx.) is the most widely distributed native North American tree (Little 1971). Its values include commercial timber production, aesthetics, and wildlife habitat (Crouch 1981). Within the Rocky Mountain region, aspen usually reproduces asexually through suckering following destruction of existing trees (Mueggler 1988). During the last century, there has been little regeneration of aspen, probably because fires have been prevented and suppressed (Crouch 1981). Without regeneration, most aspen stands eventually are invaded and replaced by conifers (Mueggler 1988). Exceptions may be high elevation aspen stands found in mesic sites between moist meadows and Douglas fir (*Pseudotsuga menziesii*) (Marr 1961). The succession of aspen to conifers, along with decreased regeneration of aspen, could lead to future landscapes composed of isolated stands of aspen within large tracts of coniferous forest.

Use of aspen communities by birds for breeding and feeding habitat is well documented (Flack 1976, Winternitz 1980, DeByle 1985, Yahner 1991). Several studies have shown that aspen forests generally support greater bird species richness and total abundance of birds than do other North American montane habitats (Salt 1957, Winternitz 1976, Reynolds

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and Finch 1988). DeByle (1985) listed 134 bird species that use aspen habitats, and aspen may be required habitat for species such as the Red-naped Sapsucker (*Sphyrapicus nuchalis*), Warbling Vireo (*Vireo gilvus*) and MacGillivray's Warbler (*Oporornis tolmiei*) (Reynolds and Finch 1988).

Bird species richness in aspen communities probably varies with the degree of isolation of stands as predicted by MacArthur and Wilson's theory of island biogeography (MacArthur and Wilson 1967). Based on that theory, one would expect lower species richness in more isolated habitats. Although the use of aspen for timber products is increasing, the main reason for harvesting aspen in Colorado is to increase regional vegetation diversity by stimulating aspen growth (D. Lowry, USDA For. Serv., pers. comm.). Most aspen stands that are harvested are four hectares or less. This size represents the majority of stands found along the front range, although larger stands can be found in southwestern Colorado. Current management of aspen in the Arapaho and Roosevelt forests of Colorado, involving the cutting of small stands (<4 ha) (D. Lowry, USDA For. Serv., pers. comm.), could lead to landscapes that support only isolated pockets of aspen in a matrix of other vegetation types. The following research was developed to investigate the effects of isolation on bird species richness in aspen stands.

STUDY AREA AND METHODS

Fourteen aspen stands were selected in Rocky Mountain National Park (RMNP) for this study. RMNP is located along the Continental Divide, adjacent to Estes Park, Colorado. Elevations range from 2438 to 4345 m. The landscape is composed mostly of glacier-sculpted valleys, rugged peaks, montane and subalpine forests, and alpine tundra (U.S. National Park Service 1988). This study area was selected because aspen stands within the Park are not currently managed. We assume the stands are undisturbed by humans and have naturally evolved to their current form.

Only 0.5% of the Park's 107,980 ha is dominated by aspen (*Populus tremuloides* Michx.) (R. Thomas, USDI Natl. Park Serv., pers. comm.). The understory in aspen groves consists mainly of common juniper (*Juniperus communis*), barberry (*Mahonia repens*), kinikinnick (*Arctostaphylos uva-ursi*), Wood's rose (*Rosa woodsii*), huckleberry (*Vaccinium* spp.), strawberry (*Fragaria* spp.), heartleaf arnica (*Arnica cordifolia*), golden banner (*Thermopsis divaricarpa*), sedges (*Carex* spp.), fescues (*Festuca* spp.), and geranium (*Geranium* spp.). Aspen habitats in RMNP have been used heavily by elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) for food and shelter (Stevens 1976). Effects of ungulate grazing on bird community structure within aspen habitats of RMNP are not known. In addition, since 1978, fire suppression has retarded the regeneration of aspen habitats within the Park. However, prescribed fires, with the sole purpose of rejuvenating aspen habitats, are included in the 1994 management plans (J. Conner, pers. comm.).

Aspen stands initially were selected using RMNP data in a geographic information system (GRASS#4.0; USACERL 1991). These data were used to generate maps of aspen stands that were categorized by diameter class (dbh) and percent canopy closure (% cc). We at-

tempted to select stands that varied in their degree of isolation from other aspen stands but were similar in area, elevation, and vegetation structure. Fourteen study stands were selected based on the following criteria: (1) average dbh >10 cm, (2) % cc >60%, (3) at least ¾ of the stand perimeter surrounded by conifers, mainly lodgepole pine (*Pinus contorta*), (4) elevation between 2500 m and 3500 m, (5) stand area 1–2 ha, (6) varying degrees of isolation from other aspen, and (7) within 2 km access from a trail or road. Many of the stands initially selected from these maps were eliminated after ground-truth surveys indicated they did not meet the above criteria. Additional stands were located using aerial photos which proved to be more useful in locating small isolated aspen stands than was the GIS database.

We surveyed each aspen stand three times for birds during June 1993. Data on species identity, number, and distance from observer were recorded for all birds seen or heard at the center of each stand and at a point located at least 100 m outside of each stand in the surrounding conifer forest, using variable circular plots (Reynolds et al. 1980). The conifer surveys were included to confirm that surrounding bird communities were similar around all 14 aspen stands. Surveys began after sunrise and continued until 11:00 h MST. Following a one-min rest period, a 10-min counting period was conducted at each point. Birds flying above the stands were not recorded.

We measured a variety of stand structural characteristics, as described below, to ensure that we selected aspen stands with similar structures. Plant species composition was not estimated because bird distributions and abundances generally are more closely correlated with habitat physiognomy (Anderson and Shugart 1974, Roth 1976, Cody 1981).

Vegetation was sampled at six random points within each aspen stand during June 1993. Random points were chosen by gridding each stand, then randomly picking coordinates within the grid. Sampling employed both line transects and 15-m radius circles. Canopy closure (>5 m), sub-canopy cover (2–5 m), shrub cover (0.5–2 m), and ground cover (<0.5 m) were sampled by noting the presence or absence of vegetation every 3 m along each of three, 15-m transects initiated at each random point. Each transect orientation was based on a reading from a secondhand watch. The reading was converted to degrees by adding a zero. Percent water cover was also recorded because Winternitz (1980) observed a correlation between the presence of standing water and high bird species richness and breeding bird density in aspen habitats of Colorado. Canopy height was estimated by taking a clinometer reading for one aspen tree at each random point. All trees located within a 15-m radius circle surrounding each random point were counted and placed into one of five diameter classes: 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, and >30 cm. This information was used to estimate stand basal area, snag basal area, mean diameter, and percent aspen within each stand (Mueller-Dombois and Ellenberg 1974).

Area of each stand was estimated, as were the areas of and distances to all other aspen stands within 1500 m of each study site. Areas and distances were estimated by digitizing 1987 aerial photos in ARC/INFO (Environmental Systems Research Institute 1991).

Basis for 1500 m isolation distance.—Bird surveys were conducted during June, at which time all local bird species were breeding (pers. obs.). We assumed that breeding birds remained in or near their territories at this time. A distance of 1500 m was selected because it exceeds the territorial and home range diameters of most forest bird species (Brewer 1963, Schoener 1968, Kroodsma 1973, Zach and Falls 1979, Mellen et al. 1992).

Calculations for isolation effects.—Isolation effects were assessed using several different measures of isolation: (1) distance to nearest neighboring aspen stand, (2) area-weighted distance to nearest neighboring aspen stand, (3) area-weighted distances of all aspen stands within 1500 m, and (4) total area of aspen stands within 1500 m. Area-weighted distances were calculated using a negative exponential function, where species richness was assumed

Table 1

Estimates of Area, Nearest Neighbor Distance, Nearest Neighbor Area-Weighted Distance (WD), Area-Weighted Distances to All Aspen within 1500 m (WD 1500 m), and Total Area of Aspen within 1500 m for 14 Aspen Sites

Site	Area (ha)	Distance (m)	WD	WD 1500 m	Total (ha)
E1	2.6	35	2.69	5.2	34
E2	1.4	63	0.66	3.8	23
E3	0.8	44	0.70	4.6	25
E4	1.4	63	1.48	4.6	21
E5	1.3	344	0.17	1.8	14
W1	1.1	74	1.59	7.4	53
W2	3.9	425	1.08	2.3	50
W3	3.2	493	0.28	2.0	21
W4	5.0	123	0.48	5.6	59
W5	1.0	218	0.41	0.6	3
W6	0.8	218	0.51	0.8	4
W7	1.9	80	1.72	4.9	27
W8	2.2	37	0.71	5.8	26
W9	2.1	13	0.77	6.4	26

to decline exponentially as distance increased. We assumed that 1% of birds present in aspen stands dispersed greater than 1500 m during the breeding season. Using this assumption, the relationship between species richness and isolation distance is: $0.01 = \exp(K \times \text{distance}_{max})$, where: $\text{distance}_{max} = 1500$ m, and K = slope of negative exponential function. Solving this equation for K gives a value of −0.0031. A weighted distance value (V) for each stand was calculated as $V = \exp(KD)$, where: $K = -0.0031$ and D = distance to the nearest neighboring aspen stand (m). An area-weighted distance (WD) was calculated as WD = VA, where V = weighted distance value and A = area of the nearest neighboring aspen stand (ha). An area-weighted isolation index incorporating all aspen stands within 1500 m (WD 1500 m) was then calculated by summing the area-weighted distances to all stands within 1500 m.

Table 1 lists the area and estimates of the various isolation measures for each aspen stand. Area-weighted isolation indices with low values represent stands that were isolated and/or had small amounts of surrounding aspen. Conversely, high values represent stands that were not isolated and/or had large amounts of surrounding aspen. The area-weighted isolation index provides an estimate of the effective or "nearby" area of available habitat. This index should be related to the expectation of dispersal for breeding birds within aspen habitat. Aspen stands with high "nearby" area estimates would be expected to maintain greater species richness than stands with low "nearby" areas.

The isolation indices calculated above, along with vegetation parameters, were incorporated into several stepwise multiple regressions (PROC REG; SAS Institute, Inc. 1987) to investigate the effects of isolation on bird species richness in aspen habitats. Vegetation parameters and isolation categories were used as independent variables and bird species richness as the dependent variable. Because several isolation categories correlated with each other, separate stepwise multiple regressions were run using each of the following isolation categories: (1) distance to nearest neighboring aspen stand, (2) area-weighted distance to

TABLE 2
MEANS AND RANGES FOR ALL VEGETATION PARAMETERS SURVEYED IN 14 ASPEN STANDS

Parameters	Mean	Range
Diameter (cm)	15.6	13.2–20.3
Height (m)	12.4	9.8–15.8
Water cover (%)	4.1	0–24.2
Ground cover (%)	59.3	34.5–83.2
Shrub cover (%)	16.3	1.2–31.0
Sub-canopy cover (%)	7.5	0–24.3
Canopy closure (%)	65.5	54.7–81.3
Aspen (%)	82.3	59.2–94.5
Basal area (m^2)	762.4	527.9–1560.3
Snag basal area (m^2)	77.6	29.5–184.2

nearest neighboring aspen stand, (3) area-weighted distances of all aspen stands within 1500 m, and (4) total amount of aspen stands within 1500 m. Stepwise multiple regressions were also done using area-weighted distances of all aspen stands and total amount of aspen stands within 500 m and 1000 m. Vegetation parameters among stands were compared using the Kruskal-Wallis nonparametric test (PROC ANOVA; SAS Institute, Inc. 1987). A separate average species richness estimate was calculated for each aspen stand and the surrounding conifers based upon three bird counts. Differences in bird species richness among aspen stands and conifers were tested by analysis of variance (PROC ANOVA; SAS Institute, Inc. 1987). Frequency distributions of bird species richness for aspen and conifer birds were compared by calculating a Kolmogorov-Smirnov test statistic (PROC NPAR1WAY; SAS Institute 1987).

RESULTS

Aspen stands were located throughout RMNP, with five on the east side of the Park and nine on the west side. All vegetation parameters were significantly different ($P < 0.01$) among the 14 stands (Table 2). Aspen stands satisfied all initial selection criteria except for stand area. Stand areas differed substantially, ranging from 0.8 ha to 5.0 ha (Table 1). Regression analysis of stand area and bird species richness was non-significant ($P = 0.62$); therefore, we assumed that species richness was not affected by differences in stand areas of the 14 aspen stands studied. Elevations for the 14 stands ranged from 2500 m to 3100 m. The distance between a stand and its nearest neighboring aspen stand ranged from 13 m to 493 m (Table 1). The total area of surrounding aspen stands within 1500 m varied between 3 ha and 59 ha (Table 1).

A total of 23 and 15 bird species were observed in aspen and conifer forests, respectively (Table 3). The most abundant species in aspen were Mountain Chickadee (scientific names in Table 3), American Robin, and

TABLE 3

BIRD SPECIES OBSERVED IN BOTH ASPEN AND CONIFER HABITATS, THE NUMBER OF STANDS EACH SPECIES WAS OBSERVED IN, AND THE TOTAL MINIMUM NUMBER OBSERVED

Species	Aspen		Conifer	
	Stands	Minimum[a] individuals	Stands	Minimum individuals
Broad-tailed Hummingbird (*Selasphorus platycercus*)	9	11	9	12
Northern Flicker (*Colaptes auratus*)	1	1	0	0
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	4	6	0	0
Hairy Woodpecker (*Picoides villosus*)	2	3	0	0
Downy Woodpecker (*P. pubescens*)	0	0	1	1
Olive-sided Flycatcher (*Contopus borealis*)	1	2	0	0
Empidonax spp.	4	4	1	1
Western Wood-Peewee (*Contopus sordidulus*)	3	3	0	0
Tree Swallow (*Tachycineta bicolor*)	2	3	0	0
Gray Jay (*Perisoreus canadensis*)	2	2	3	5
Jay spp.	1	1	0	0
Black-capped Chickadee (*Parus atricapillus*)	2	2	1	1
Mountain Chickadee (*P. gambeli*)	12	26	8	13
Chickadee spp.	3	3	2	3
Red-breasted Nuthatch (*Sitta canadensis*)	1	2	1	1
Brown Creeper (*Certhia americana*)	1	2	1	2
House Wren (*Troglodytes aedon*)	3	5	0	0
Ruby-crowned Kinglet (*Regulus calendula*)	7	8	8	11
American Robin (*Turdus migratorius*)	13	22	8	10
Warbling Vireo (*Vireo gilvus*)	12	20	4	5
Yellow-rumped Warbler (*Dendroica coronata*)	9	10	8	10
Sparrow spp.	2	2	0	0
Dark-eyed Junco (*Junco hyemalis*)	12	15	13	17

TABLE 3
CONTINUED

Species	Aspen		Conifer	
	Stands	Minimum[a] individuals	Stands	Minimum individuals
Brewer's Blackbird (*Euphagus cyanocephalus*)	1	1	0	0
Pine Siskin (*Carduelis pinus*)	4	5	5	7
Red Crossbill (*Loxia curvirostra*)	0	0	1	1
Finch spp.	1	1	0	0
Unidentified	13	24	13	21

[a] Minimum number of individuals was determined to be the greatest number of individuals seen during any one of three counting periods.

Warbling Vireo. The most abundant species in conifer were Mountain Chickadee, Broad-tailed Hummingbird, and Ruby-crowned Kinglet.

The majority of species occurred in only one or two sites (Fig. 1). No species was seen in all 14 aspen or 14 conifer sites. The above distributions were non-significant ($K_{sa} = 0.6$, $\alpha = 0.05$), indicating that the frequency distributions of bird species richness for aspen and conifer birds were similar. Bird species richness differed significantly ($P = 0.003$) among the 14 aspen stands. Differences in bird species richness among conifer sites were also tested and were non-significant ($P = 0.40$, power $[1 - \beta] = 0.49$). Average bird species richness was significantly higher in aspen than in conifer habitats ($P < 0.0005$).

All stepwise multiple regressions selected one-variable models, with percent shrub cover (0.5–2 m height) as the only significant predictor variable. Variation in the density of the shrub understory accounted for 58% of the variance in bird species richness ($R^2 = 0.58$, $r = 0.76$) (Fig. 2). The prediction equation was: $\hat{y} = 5.13 + 0.16$ (shrub cover).

DISCUSSION

Our results show a high degree of variability in vegetation structure among aspen stands in RMNP. Although vegetation parameters varied among stands, certain parameters appear to be more influential than others in determining bird community structure. In this study, the amount of understory vegetation appeared to be the main determinant of bird species richness. The presence of vegetation in the shrub layer may benefit birds by providing cover and increasing food availability. Percent shrub cover (0.5–2.0 m height) was highly correlated with bird species richness ($r =$

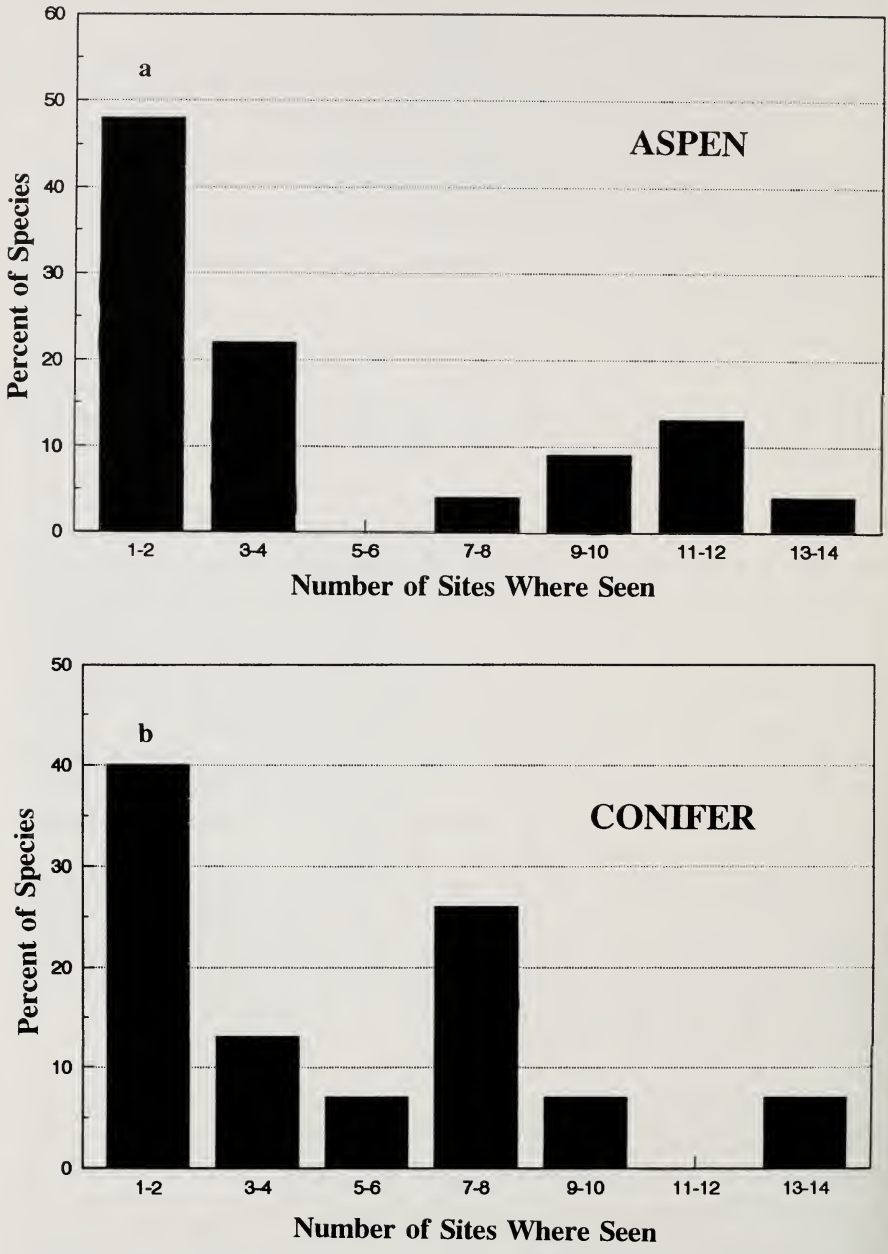

FIG. 1. Percent of all species that were seen in (a) 14 aspen sites and (b) 14 conifer sites in RMNP, Colorado.

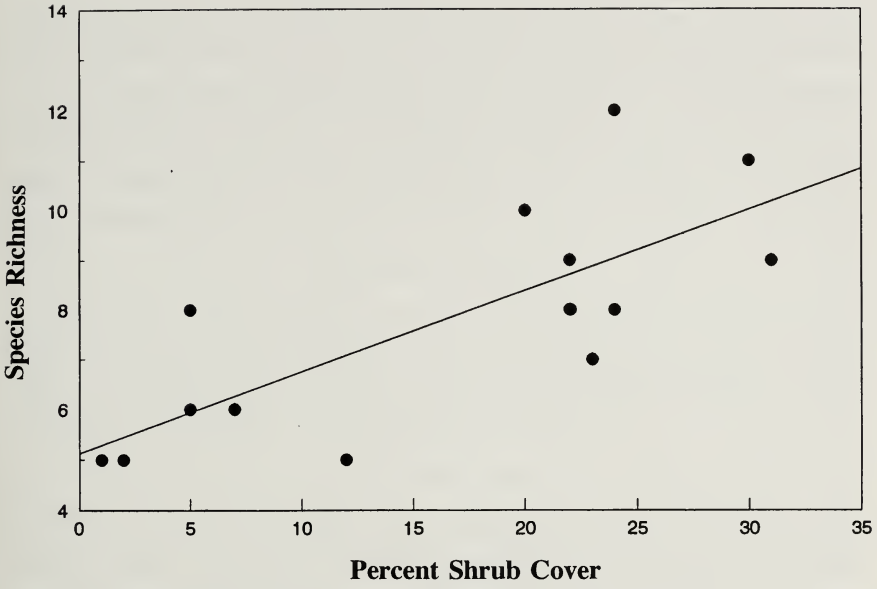

FIG. 2. Regression of shrub cover (0.5–2 m height) and bird species richness (P = 0.0015; R^2 = 0.58).

0.76, P = 0.0015). A recent study by Mills et al. (1991) reported a strong correlation between total vegetation volume and breeding bird density. This suggests that bird density and species richness may reflect the overall abundance of resources. Our results corroborate such suggestions.

On average, aspen sites contained a higher species richness than did surrounding conifer sites. Eight species were observed in aspen that were not observed in conifer: Northern Flicker, Red-naped Sapsucker, Hairy Woodpecker, Olive-sided Flycatcher, Western Wood-Peewee, Tree Swallow, House Wren, and Brewer's Blackbird. Some of these species, such as the Red-naped Sapsucker may require aspen for survival and reproduction (Reynolds and Finch 1988). Therefore, even small stands of aspen, such as those studied, may be important in supporting populations of birds that require aspen for survival and reproduction, thus maintaining the overall species richness in the landscape.

Isolation had no significant effect on bird species richness within the 14 aspen stands studied. Several hypotheses may explain these results: (1) isolation distances greater than the maximum considered here (493 m) may be necessary before isolation effects are observed, (2) other factors which were not studied may overshadow the effects of isolation (e.g., predation rates, competition, food availability, disease), (3) bird species

richness may be more influenced by vegetation structure than by isolation, and/or (4) isolation does not influence bird species richness in aspen communities because this habitat is intrinsically highly fragmented.

Previous studies of isolation effects on bird species richness produced varying results. Johns (1993) observed that the presence of forest interior bird species was influenced by both aspen grove size and isolation. Whitcomb et al. (1981) stated that isolation was an important factor in determining the presence of forest interior bird species in lowland deciduous forests in Maryland. Yet, Lynch and Whigham (1984) showed that the species richness of forest interior birds in Maryland was related only to area and isolation when differences in vegetation were controlled. Martin (1980) concluded that area was more important than isolation or vegetation structure in determining bird abundance and species richness in shelterbelts of South Dakota. A decline in the bird species richness of pine forests in France was shown to coincide with decreasing patch size and increasing isolation (Lescourret and Genard 1994). Lescourret and Genard believed the effect could be attributed to a variation in vegetation structure and altitude. Isolation was shown to affect bird species richness negatively in forest islands in Wisconsin once area effects had been taken into account (Howe 1984).

Our limited evidence suggests that other habitat variables, notably habitat structure, may be more important than habitat isolation in determining bird species richness in aspen communities of Colorado. Furthermore, species-specific isolation effects may not be reflected by changes in overall species richness. Since species respond differently to habitat variations, isolation effects may be more appropriately studied by investigating individual species. This was not attempted in this study because of limited numbers of observations for most species.

Although the results from this study suggest that isolation had little effect on the bird species richness of small aspen stands, the effect of isolation on individual species needs to be investigated. Until species-specific data are obtained, managers should not disregard the possible influence of habitat isolation on bird communities. We recommend that population studies focus on some or all of the eight species we observed only in aspens.

Because bird species richness correlated significantly with shrub cover ($r = 0.76$), we would recommend management techniques that maintain or produce abundant understory vegetation in aspen habitats. Understory development might be enhanced by controlling grazing pressure by elk and mule deer.

This study begins to investigate the effects of landscape patterns on bird species richness. Further studies which employ manipulation of land-

scape patterns and long-term monitoring of trends in bird species occurrence should be supported. Areas with highly isolated aspen habitats and areas with non-isolated habitats should be compared over several decades for differences in species abundances, composition, and richness. The survivorship and fitness of individuals among isolated and non-isolated habitats should also be investigated before the true effects of isolation may be known.

ACKNOWLEDGMENTS

A grant for this project was provided by the Boone and Crockett Club. We thank Linda Bourgeois for assistance in the field, John Bustos and Dennis Lowry from the USDA Forest Service for advice and support, and Craig Axtell, Cheryl Arnt, and Ron Thomas of Rocky Mountain National Park for GIS support and lodging. The manuscript benefited from the comments of B. L. Winternitz and an anonymous reviewer.

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Wilson Bull., 107(3), 1995, pp. 475–484

BREEDING BIOLOGY OF FLORIDA PRAIRIE WARBLERS AND CUBAN YELLOW WARBLERS

JOHN W. PRATHER AND ALEXANDER CRUZ

ABSTRACT.—We studied the breeding biology of the Florida Prairie Warbler (*Dendroica discolor paludicola*) and the Cuban Yellow Warbler (*D. petechia gundlachi*) in black mangrove (*Avicennia germinans*) habitats in the Florida Keys. A total of 42 Prairie and 20 Yellow warbler nests was located during 1990–1993. The breeding season for both species extended from late April through early July. The two species used a similar range of nest heights and placed their nests in similar locations within the mangroves, but Yellow Warbler nests averaged higher (1.77 m) than Prairie Warbler nests (1.60 m) and were less likely to be placed against mangrove trunks. Incubation periods averaged 12 days for both warblers. Brooding periods averaged 11 days for Prairie Warblers and 12 days for Yellow Warblers. These periods are equivalent to or slightly longer than typical periods for other races of Prairie and Yellow Warblers that breed in North America, and similar to those for races of Yellow Warblers that breed in the West Indies. Mean clutch sizes for Prairie Warblers (2.50, N = 29) and for Yellow Warblers (2.50, N = 16) are smaller than those for temperate races of these warblers. Fledging success (number of young fledged/number of eggs laid) was higher for the Yellow Warbler (65.0%) than for the Prairie Warbler (45.8%), but the number of young fledged per nest did not differ significantly between the two species. Predation was the major cause of nest failure, accounting for approximately 64% of all egg losses. *Received 15 Nov. 1994, accepted 28 Feb. 1995.*

Two distinct subspecies of wood warblers (Family Emberizidae, subfamily Parulinae) breed in the mangrove habitats of south Florida. The Florida Prairie Warbler (*Dendroica discolor paludicola*) is a Florida endemic, breeding only in the Florida Keys and along the southern and central Florida coast. The Cuban Yellow Warbler (*D. petechia gundlachi*) was first recorded breeding in the Florida Keys in 1941 (Greene 1942), and it is now resident in the keys and along the south Florida coast (Robertson and Woolfenden 1992). Cuban Yellow Warblers are found elsewhere only in the Bahamas and Cuba (Robertson 1955, Bond 1956).

Both the Florida Prairie Warbler and the Cuban Yellow Warbler have been designated "species of special concern" in Florida due to their limited range and threats to their mangrove habitats such as development, human disturbance, and hurricanes (Kale 1978). In addition, two species of brood-parasites, the Brown-headed Cowbird (*Molothrus ater*) and the Shiny Cowbird (*M. bonariensis*), have recently invaded the south Florida region (Cruz et al. 1989, Cruz et al. unpubl. data) and may affect the breeding success of these warblers in the future. As part of a larger study,

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baseline data on the breeding biology of Prairie and Yellow warblers were gathered during spring and summer 1990–1993.

STUDY AREA AND METHODS

Study sites.—This study was carried out in mangrove forests on south Key Largo, Florida, and on several small, mangrove dominated keys in Florida Bay, just offshore from Key Largo. The dominant vegetation in all of the sites was black mangrove (*Avicennia germinans*), comprising between 70% and 100% of the woody vegetation. Other woody plants in some sites included red mangrove (*Rhizophora mangle*), buttonwood (*Conocarpus erecta*), and sea grape (*Coccoloba uvifera*). In some sites, the mangroves occurred in clumps surrounded by open areas subject to tidal fluctuations. Mangroves in these areas rarely exceeded 2.5 m in height. In other sites, the mangroves averaged 3 to 5 m tall and formed a moderately dense woodland with a closed canopy. A sparse understory of the succulent saltwort (*Batis maritima*), grasses (*Monanthochloe littoralis, Sporobolus* sp.), and black mangrove aerial roots (pneumataphores) was present in the study sites.

Nest placement.—Nests were located by searching mangrove trees and shrubs and by locating and following warblers that were actively constructing nests. In some cases, nests contents were examined by climbing trees. For each active nest, the substrate in which the nest was placed, the nest height, and the location of the nest were recorded. Data were not recorded on inactive nests because of the similarity between Prairie and Yellow warbler nests; inactive nests could not be attributed to one species with 100% certainty. A two-tailed Mann-Whitney *U*-test was used to determine if there were differences in the nesting heights of Florida Prairie Warblers and Cuban Yellow Warblers.

Timing of breeding.—Each site was searched for new nests every two to three days during June 1990 and 1991, late March to early July 1992, and late April through early August 1993. For each nest, the dates of laying of the first egg, hatching of the young, and fledging of the young were recorded, when these were known.

Reproductive biology.—After a nest was located, it was checked every two to three days until it failed or young were successfully fledged. Most nests were located in the nest-building or incubation periods, but a few were located when the young had already hatched. Nest contents were recorded at the time of each check, and the data were used to determine incubation periods, clutch sizes, and nesting successes.

Incubation periods were determined by measuring the time, to the nearest day, from the date of the laying of the last egg to the date of hatching for the last egg to hatch. The period was assumed to include the date of laying but not the date of hatching. Brooding periods were determined by measuring the time, to the nearest day, between the hatching of the last egg and the fledging of the young. The period was assumed to include the date of hatching but not the date of fledging. Only nests in which the exact dates of laying, hatching, and fledging were known, and in which all eggs hatched and all young fledged were analyzed.

Clutch sizes were determined using 29 Prairie Warbler nests and 16 Yellow Warbler nests found before egg laying began, or during the egg laying or early incubation periods. It is possible that eggs were lost from some of these nests before they were found, but this seems unlikely. Loss of individual eggs, rather than the complete clutch, was only noted in one nest out of the 28 found before laying began. All of these nests, therefore, were assumed to hold complete clutches. A two-tailed Students *t*-test was used to determine if there were significant differences in the mean clutch size for Florida Prairie Warblers and Cuban Yellow Warblers.

Hatching and fledging success were determined using the same 29 Prairie Warbler nests and 16 Yellow Warbler nests. Hatching success was defined as the number of young hatched

divided by the number of eggs laid in those nests. Fledging success was defined as the number of young fledged divided by the number of eggs laid. The status of each nest was checked every two to three days until the nest failed or the young fledged. If the nest failed, the date of failure was noted and the area was searched for evidence of the cause of failure. If the nest produced fledglings, the date was noted and the number of young fledged was verified by locating and counting the fledglings. In a few cases some of the fledglings could not be located near the nest. In those cases all of the young in the nest at the time of the previous check were assumed to have fledged. A chi-squared test with continuity correction was used to determine if there were differences in the proportion of young fledged/eggs laid for Prairie Warblers and Yellow Warblers. A two-tailed Students *t*-test was used to determine if there were differences in the number of young fledged per nest for Prairie and Yellow warblers.

RESULTS

Nest placement.—All Prairie Warbler (42) and Yellow Warbler (20) nests were located in black mangrove trees or shrubs. There was a significant difference in the overall nesting heights of Prairie and Yellow warblers, with Yellow Warbler nests being placed higher on average than Prairie Warbler nests ($P = 0.038$). Prairie and Yellow warblers used essentially the same range of nesting heights, however. Prairie Warbler nests ranged from 0.30 m to 4.62 m above ground level, averaging 1.60 ± 1.02 m above the ground. Yellow Warbler nests averaged 1.77 ± 0.77 m above ground level, ranging from 0.37 m to 4.51 m above the ground.

Of 42 Prairie Warbler nests, 20 (48%) were located in forks formed by two or more twigs, 14 (33%) were located on the top of horizontal or diagonal branches, and eight (19%) were located against trunks. Yellow Warbler nest placement was similar to that of Prairie Warblers, with 12 of 20 (60%) nests located in forks formed by vertical twigs, and 7 of 20 (35%) nests located on horizontal or diagonal branches. Only one Yellow Warbler nest (5%) was found against a trunk.

Timing of breeding.—Egg laying occurred between May 4 and June 25 in 19 Prairie Warbler nests and between May 20 and June 12 in nine Yellow Warbler nests for which the date of laying of the first egg was known. In 1993, one Yellow Warbler nest fledged young on May 17, and one Prairie Warbler nest fledged young on May 23, indicating that some birds began nesting in late April of that year. Hatching of eggs of both species typically occurred between May 18 and June 24. Eggs in one Prairie Warbler nest hatched around July 3, this being the latest recorded date of hatching for either species. Fledging of warblers typically occurred between June 5 and July 5.

Incubation and brooding periods.—The period between the laying of the first egg and the hatching of the last egg to hatch varied between 12 and 18 days (average 14.5) in six Prairie Warbler nests and between 12 and 16 days (average 14) in six Yellow Warbler nests. Neither female

TABLE 1
SUCCESS OF PRAIRIE WARBLER AND YELLOW WARBLER NESTS

Nest data	Species	
	Prairie Warbler	Yellow Warbler
Number of nests	29	16
Average clutch size	2.86	2.50
Number of eggs laid	83	40
Number of eggs hatched	41	29
Number of young fledged	38	26
Hatching success[a]	49.4%	72.5%
Fledging success[b]	45.8%	65.0%
Number of fledglings/nest	1.31	1.62

[a] Number of eggs hatched/number of eggs laid.
[b] Number of young fledged/number of eggs laid.

Prairie Warblers nor female Yellow Warblers incubated the eggs until the last egg was laid, and both laid one egg per day. The average period of incubation for both Prairie Warbler and Yellow Warbler eggs was 12 days (range 10–15 days).

The period between the hatching of the last egg and the fledging of the young varied from 10 to 14 days in the same 12 warbler nests mentioned above. The brooding period averaged 11 days for Prairie Warblers and 12 days for Yellow Warblers. Only female warblers brooded the young, but both males and females fed nestlings. Adding both incubation and brooding periods together gives an average time of 23 days for nest attentiveness of Prairie Warblers and 24 days of nest attentiveness of Yellow Warblers.

Clutch sizes.—Mean clutch size was 2.86 ± 0.69 eggs for Florida Prairie Warblers and 2.50 ± 0.73 eggs for Cuban Yellow Warblers (Table 1). Of the 29 Prairie Warbler nests in which a full clutch was known or assumed to have been laid, five (17%) contained four eggs, fifteen (52%) contained three eggs, and nine (31%) contained two eggs. Of the 16 Yellow Warbler nests in which a full clutch was known or assumed to have been completed, one (5%) contained four eggs, seven (35%) contained three eggs, seven (35%) contained two eggs, and one (5%) contained only one egg. There were no significant differences in the mean clutch size of the two species ($P = 0.107$).

Nesting success.—In nests in which a full clutch was known or assumed to have been completed, 41 of the 83 eggs (49.4%) laid by Prairie Warblers were successfully hatched, while 29 of the 40 eggs (72.5%) laid by Yellow Warblers were successfully hatched (Table 1). Of the 41 Prairie

Warblers that successfully hatched, 38 (92.7%) were successfully fledged, and of the 29 Yellow Warblers that hatched, 26 (89.7%) were successfully fledged (Table 1). Overall rates of nesting success (number of eggs laid/ number of young fledged) were 45.8% for the Florida Prairie Warbler and 65.0% for the Cuban Yellow Warbler (Table 1). In all 13 (45%) of the 29 Prairie Warbler nests and 12 (75%) of the 16 Yellow Warbler nests produced at least one young. The mean number of fledged young per nest was 1.31 for Prairie Warblers and 1.62 for Yellow Warblers. No significant differences were found in the number of young fledged per nest by the two species ($P = 0.258$), but a significantly higher percentage of Yellow Warblers fledged per egg laid ($P = 0.026$).

Predation was the major cause of nest failure for both species. Twenty-seven Prairie Warbler eggs in 10 nests and seven Yellow Warbler eggs in three nests were believed to have been lost to predators during the course of this study. This accounts for 64.3% of the egg losses by Prairie Warblers and 63.6% of the egg losses by Yellow Warblers. A higher percentage of Prairie Warbler eggs (35.9%) than Yellow Warbler eggs (17.5%) were lost to predators. Evidence for egg loss to predators included animal tracks (rat [*Rattus* sp.] and raccoon [*Procyon lotor*]) at the nest site, punctured or crushed eggs in or near the nest, and nests damaged in ways consistent with a predation event. In three cases, eggs disappeared from nests without a trace and were thought to have been lost to snakes. Probable nest predators included rats, raccoons, Red-winged Blackbirds (*Agelaius phoeniceus*) and mangrove water snakes (*Nerodia compressicauda*). Strong et al. 1991 found that the White-crowned Pigeon (*Columba leucocephala*) nesting distribution on the Florida Keys appeared to be limited by the presence of raccoons. Of the 33 keys on which they found evidence of raccoons, only six had nesting White-crowned Pigeons.

Failure of eggs to hatch and, in some cases, subsequent nest abandonment were also significant factors in reduced nesting success of the Prairie Warbler. Ten of 83 (12.1%) Prairie Warbler eggs failed to hatch, whereas only two of 40 (5.0%) Yellow Warbler eggs failed to hatch. Other, less important causes of reduced nesting success included storms that damaged nests, young falling from the nest, and death of hatchlings in the nest. A total of eight eggs or young were lost by Prairie Warblers and five eggs or young were lost by Yellow Warblers due to these circumstances. Cowbirds (*Molothrus* spp.), which could reduce warbler nesting success through brood parasitism, were seen near the area of this study, but no evidence for brood parasitism was found in the study sites.

DISCUSSION

The breeding biology of Florida Prairie Warblers and Cuban Yellow Warblers are very similar in most aspects. Both species also showed a

high degree of resource overlap and occasionally occurred in overlapping territories (Prather and Cruz, unpubl. data). These results are not surprising because the two species are closely related and occur in the same habitats.

Nest placement.—Both Florida Prairie Warblers and Cuban Yellow Warblers seem to prefer to nest in black mangroves, which comprised approximately 90% of the woody vegetation in our study sites. In other Florida habitats, where the composition of the vegetation differs, they have been recorded nesting in other substrates (Stevenson and Anderson 1994). Harrison (1981) found Prairie Warblers in wax myrtle (*Myrica cerifera*) bushes on Sanibel Island, and Bent (1953) reported that Prairie Warbler nests have been found in red mangroves. Cuban Yellow Warblers have also been reported nesting in red mangroves in Florida (Greene 1942, Sprunt 1954). In Puerto Rico, in areas where black mangroves were the predominant woody vegetation, 55 of 57 Yellow Warbler nests found by Wiley (1982) were placed in black mangroves.

The differences in nesting height and nest placement by Prairie and Yellow warblers in black mangroves seem to represent species preferences rather than real differences in nest site selection. A study of multiple habitat variables, including substrate height, mean vegetation height, and mean percentage canopy cover in plots around warbler nest sites revealed no significant differences in nest site selection between the Florida Prairie Warbler and the Cuban Yellow Warbler (Prather and Cruz, unpubl. data). Furthermore, comparison of habitat variables in nest plots with the same variables in randomly placed plots suggested both species chose nest sites randomly with respect to the habitat (Prather and Cruz, unpubl. data).

Timing of breeding.—Florida Prairie Warblers and Cuban Yellow Warblers may become territorial and begin singing as early as mid-January in south Florida (W. Hoffmann, pers. comm.). Active Prairie Warbler nests have been recorded as early as March 29 (Howell 1932) and as late as September 2 (Atherton and Atherton 1987). Despite being in the study areas in early April 1992 and late April 1993, we found no active warbler nests before the beginning of May. Two nests containing young were found in mid-May 1993, however, indicating a few birds began laying eggs in late April of that year. No warbler nests containing eggs were located after mid-June, but two Prairie Warbler nests fledged young in July. Historically, 18 sets of Florida Prairie Warbler eggs were collected during May and June (Stevenson and Anderson 1994), and many observers have reported finding active Prairie Warbler nests during this period (Howell 1932, Sprunt 1954, Harrison 1981, Stevenson and Anderson 1994). Greene (1942) found a Yellow Warbler nest with one egg on June

26, 1941. Therefore, most Prairie and Yellow warblers in Florida appear to breed between late April and early July.

A three month breeding season would give both species enough time to raise two broods. Only one such instance was noted, however. In at least two other cases, one involving Prairie Warblers and one involving Yellow Warblers, a pair renested after an initial nest failure. Northern Prairie Warblers that successfully raised a first brood have been found to have second broods about 21% of the time (Nolan 1978). It is not known if Cuban Yellow Warblers have second broods, but some other Yellow Warbler races do (Bent 1953).

It is as yet unknown what factors affect the timing of breeding in Florida. One possibility is that migratory insectivorous birds that winter in Florida may depress the resource availability in mangroves enough to prevent breeding while they are present, primarily September to May (National Audubon Society Records, Lane 1992). Another possibility is that the timing of breeding is affected by the seasonal rainfall patterns. In Puerto Rico, Yellow Warblers typically breed in mangrove habitats between March and August (Wiley 1982; Nakamura and Cruz, unpubl. data), but the breeding season varies from year to year in response to increases in insect abundance caused by rains. Brief early summer rains in April and May often cause a flush of mosquitoes and probably other insects in the Florida Keys (pers. obs.). On the other hand, heavy rains later in the summer damaged or destroyed at least five warbler nests that were subsequently abandoned, and Yellow Warblers have been known to abandon nests during heavy rains in Puerto Rico (T. Nakamura, pers. comm.).

Incubation and brooding periods.—The data indicate that the duration of incubation and brooding is similar for the Florida Prairie Warbler and Cuban Yellow Warbler. The periods are slightly longer than reported periods for races of the Prairie and Yellow warblers that breed at higher latitudes but similar to those reported for other races of the Yellow Warbler in the West Indies. Nolan (1978) found an incubation period ranging from 10.5 to 14.5 days (average 12 days) and a brooding period ranging from 8 to 11 days (average 9.5 days) for Northern Prairie Warblers in Indiana. Schrantz (1943) reported an average incubation period of 11 days (range 10–12 days) and an average brooding period of 9.5 days (range 8–10 days) for the Eastern Yellow Warbler (*D. p. petechia*) in Iowa. Incubation and brooding periods for races of the Yellow Warbler that breed on St. Lucia and Puerto Rico average about 11–12 days each (T. Nakamura, pers. comm.).

Clutch sizes.—Few clutch sizes for Florida Prairie Warbler nests have been reported in the literature, and those that can be considered to be

complete clutches all contained three eggs (Howell 1932, Harrison 1981). To our knowledge, no other clutch sizes for Cuban Yellow Warbler nests have been published. However, clutch size information exists for two other West Indian subspecies, *D. p. cruciana* of Puerto Rico and *D. p. babad* of St. Lucia, revealing that clutch sizes were similar to the sizes found in this study. In Puerto Rico, Wiley (1982) found an average clutch size of 2.6 ± 0.49 eggs (N = 15 nests), Nunez-Garcia (1988) found an average clutch size of 2.2 ± 0.10 eggs (N = 36 nests), and Nakamura and Cruz (unpubl. data) found an average clutch size of 2.1 ± 0.56 eggs (N = 10). In St. Lucia, Nakamura and Cruz (unpubl. data) found an average clutch size of 2.3 ± 0.61 (N = 32) for the Yellow Warbler. Clutch sizes for other species of *Dendroica* warblers from the West Indies, such as Adelaide's Warbler (*D. Adelaidae*), Olive-capped Warbler (*D. pityophila*), Vitelline Warbler (*D. vitellena*), Plumbeous Warbler (*D. plumbea*), and Arrow-headed Warbler (*D. pharetra*) typically range from two to four eggs (Bond 1936; Curson et. al 1994; Nakamura and Cruz, unpubl. data).

The general trend toward smaller clutch sizes for birds breeding in the tropics than for those breeding in temperate zones (Cody 1966), including warblers (Morse 1989), is shown by both Prairie and Yellow warblers. In Indiana, the mean clutch size for nests of the Northern Prairie Warbler that were not affected by brood-parasitism or predation (188 nests) was 3.89 ± 0.50 (Nolan 1978). Of those, 139 (74%) contained four eggs. In Kentucky, 14 Prairie Warbler clutches averaged 3.5 ± 0.14 eggs (Mengel 1965). In Illinois, 33 unparasitized nests of the Eastern Yellow Warbler (*D. p. aestiva*) contained an average of 4.0 eggs (Graber et al. 1983), and 41 nests in Iowa contained an average of 4.1 eggs (Schrantz 1943). In Manitoba, the mean clutch size was 4.5 eggs (N = 1005) (Sealey 1992). The mean clutch size for the Florida Prairie Warbler is about one egg fewer than its northern counterpart and that for the Cuban Yellow Warbler appears to be about 1.5 fewer than that for its northern relatives. It is interesting to note that the Florida Prairie Warbler, which is probably derived from temperate stock (Nolan 1978, Robertson 1955), has a slightly higher mean clutch size than the Cuban Yellow Warbler which invaded Florida from the West Indies.

Nesting success.—Overall hatching success was higher for Yellow Warblers than for Prairie Warblers (Table 1). This difference was, in part, due to predation which accounted for about 64% of both Prairie and Yellow warbler egg losses. It also appears, however, that Prairie Warblers are more likely to have infertile or inviable eggs. Two complete Prairie Warbler clutches (total 5 eggs) failed to hatch and were subsequently abandoned. Four other clutches had one egg fail to hatch, and one had two

eggs fail to hatch. Only one Yellow Warbler egg in each of two nests failed to hatch.

Once a nestling hatched from the egg, it was very likely to survive to fledging (Table 1). There are no clear reasons for this, but it may be that most of the nests that were likely to be found by predators or damaged during storms failed during incubation. Yellow Warblers showed higher hatching and fledging success than did Prairie Warblers because a lower percentage of Yellow Warbler eggs failed to hatch and Yellow Warblers were less likely to abandon a nest. Despite this, no significant differences occurred in the number of young fledged per nest by the two species. This may be due to a slightly, but not significantly, larger mean clutch size for the Prairie Warbler.

ACKNOWLEDGMENTS

We thank the National Audubon Society for all the logistical help, in particular A. Sprunt, IV, G. T. Bancroft, W. Hoffman, R. J. Sawicki, and A. M. Strong. We are grateful to the National Park Service and the United States Fish and Wildlife Service for allowing us to work within lands under their jurisdiction. C. R. Blem, C. E. Bock, H. W. Kale, and T. K. Nakamura helped to improve this manuscript through many constructive comments. Financial support was provided by the National Geographic Society and the United States Fish and Wildlife Service.

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Wilson Bull., 107(3), 1995, pp. 485–495

ARTHROPOD PREY OF NESTLING RED-COCKADED WOODPECKERS IN THE UPPER COASTAL PLAIN OF SOUTH CAROLINA

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Abstract.—Four nest cavities of the Red-cockaded Woodpecker (*Picoides borealis*) were monitored with automatic cameras to determine the prey selected to feed nestlings. Twelve adults were photographed making nearly 3000 nest visits. Prey in 28 arthropod taxa were recognizable in 65% of the photographic slides. Wood roaches in the genus (*Parcoblatta*) made up 69.4% of the prey fed to nestlings. Other common prey items were wood borer larvae (Cerambycidae or Buprestidae, 5.4%), Lepidoptera larvae (4.5%), spiders (Araneae, 3.6%), and ants (Formicidae, 3.1%). Wood roaches were the only prey items consistently taken by all four groups of birds; they made up 63.3 to 81.6% of the prey observed. Other common prey generally were taken in large numbers only by a single group of woodpeckers. During the breeding season these woodpeckers utilize relatively few common arthropods to feed nestlings. *Received 10 Nov. 1994, accepted 20 Feb. 1995.*

The endangered Red-cockaded Woodpecker (*Picoides borealis*), found throughout the south from eastern Texas to the Atlantic coast, uses live pine tree boles and branches as primary foraging substrate (Hooper and Lennartz 1981, Porter and Labisky 1986), but little is known about their food habits. Determining Red-cockaded Woodpecker prey is critical to understanding the species' foraging ecology. The purpose of this study was to develop an effective system for long-term monitoring of prey use by the Red-cockaded Woodpecker and to develop quantitative prey use data for this endangered species. We examined the diet of nestling Red-cockaded Woodpeckers as part of a larger study on the biology and ecology of insects associated with the bark of live pine trees.

METHODS

We conducted this study on the Savannah River Site (SRS), an 80,269 ha Dept. of Energy (DOE) nuclear production facility in Aiken County, South Carolina. The SRS is on the upper Atlantic Coastal Plain Physiographic Province. Its northern sector consists of uplands and sandhills where conditions are dry and the most common plant communities are longleaf pine (*Pinus palustris*) plantations and natural stands of longleaf pine and turkey oak (*Quercus laevis*). Loblolly pine (*P. taeda*) and bottomland hardwoods predominate on the more mesic areas and in riparian areas. Longleaf, loblolly, and slash (*P. elliotii*) pine stands occupy approximately 14,924 ha, 25,677 ha, and 12,011 ha, respectively (Knox and Sharitz 1990). Most of the stands are under 50 years of age. Potential Red-cockaded Woodpecker nesting

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FIG. 1. Nikon F4 camera with MF-24 multicontrol back and a Nikon SB-25 flash unit in a watertight housing constructed from an electrical box. The infrared sending unit (a) of a Trailmaster 1500 game monitor is attached to the cavity tree above the nest cavity (b) and the receiving unit (c) is attached at the base of the tree. The game monitor detects the presence of a bird at the cavity and trips the camera.

habitat is sparse on the site because only 1521 ha are in pine stands 60 years old or older. The land surrounding the centrally located nuclear production areas has limited public access and is managed by the USDA Forest Service. It contains several Red-cockaded Woodpecker groups containing breeding pairs and one-to-several associated helpers. At the SRS, every woodpecker is banded with a U.S. Fish and Wildlife Service band and a unique set of plastic colored bands. We selected four of the groups at the SRS that had successfully bred during previous years (Franzreb, unpubl. data), and we placed our cameras near their nest cavity trees.

Each of our camera systems (Fig. 1) consisted of a Nikon F4 autofocus camera with a Sigma 500-mm/f7.2 APO lens and a Nikon MF-24 multicontrol back, which held a film cassette allowing 250 exposures and imprinted the time and date of each exposure on the film. We attached a Nikon SB-25 autofocus flash with an auxiliary battery pack to increase the number of flashes between battery changes. We housed each camera in a watertight 15 × 38 × 43 cm fiberglass electrical box (Fig. 1). We cut a 9.5 × 17.5 cm hole in one side of each box and fitted it with a high quality 4-mm-thick glass pane sealed to the box with silicone caulk and held in place with mirror mounting brackets. A second hole 2.5 cm diameter was drilled in the back of the box directly behind the camera viewfinder and similarly fitted with glass. Styrofoam insulation (1.3 cm thick) was attached to the inside of the lid, back, and two sides of the boxes to provide some protection from heat and to reduce camera noise. The camera and flash were supported on separate metal brackets attached to 1.3 cm thick plywood which was fastened to the back of the boxes.

We mounted each camera unit on a 4 m tall Warren and Sweat Co. tripod style deer stand. A mounting and aiming bracket was constructed from 4 × 4 cm angle iron and 2-cm-thick plywood (Fig. 1). This arrangement allowed us to aim the camera vertically by sliding the bottom camera housing attachment bolt through an arc cut in the plywood backing of the aiming bracket. We assembled four of these camera systems and located them at

Red-cockaded Woodpecker Clusters 2, 3, 18, 19, and 39 (numerical designations used by the USDA, Forest Service, Savannah River Forest Station). Because Group 2 nested early and Group 18 was late, we were able to use the four cameras at five nest cavities.

We attached Trailmaster 1500 game monitors to the boles of the nest trees to trip the cameras (Fig. 1). The infrared sending units of the game monitors were 2–3 m above the nest cavities, and the receiving units were attached to the trees 1.5–2 m above the ground. The cameras were automatically tripped when adult birds returned to the nest cavity and interrupted the infrared beam produced by the game monitors. The Trailmaster units were factory-adjusted to have no limit on the number of photographs they would initiate. We set each unit to operate at its most sensitive level and to have a 30-sec delay after a photo was taken to minimize multiple pictures of the same feeding and to eliminate photos of adults leaving the nest with fecal sacs. The Trailmasters were programmed to operated from 06: 00 to 20:30 h EST.

We used Ektachrome 200 slide film. The shutter speed was 1/250 sec, and the autoexposure was set on shutter priority. The flash unit automatically metered existing light through the camera lens and adjusted itself for proper exposure. The rechargeable nickel cadmium batteries used in the flash units were replaced every day. The film was developed as uncut rolls, which allowed us to examine each frame in sequence. Each frame or slide was examined with a stereoscope at 12× magnification, and arthropods were identified to the lowest taxonomic level possible. Time, date, and bird identification based on leg bands was recorded for each slide. Arthropod sampling in the study area (Hanula and Franzreb, unpubl. data) and the arthropod collection at the Georgia Natural History Museum, Athens, Georgia, facilitated prey identification for this study.

We examined the frequency of visits with different prey items for all groups combined, for each woodpecker group separately, and by the age of the nestlings. In addition, we compared the frequency of visits by breeding males, breeding females, and helper males.

RESULTS

The cameras recorded over 3000 nest visits, of which 2978 were of sufficient quality to be used in the analysis. Of the usable slides, 64.5% contained identifiable prey, and 20.9% contained prey items that were visible but could not be identified conclusively. In another 9%, the prey item was not visible, either because the bird's head was turned away from the camera or because its head was already extended into the nest cavity. In 5.6% of the pictures, no food items were visible.

We identified 28 arthropod taxa as prey from the photos (Table 1). Red-cockaded Woodpeckers feed their young either a large prey item or carry a number of small prey at one time. Only rarely did we see a photo of a bird bringing one small item, such as a single roach egg case or a small spider. We used separate listings to show whether the prey consisted of single or multiple items. For example, in Table 1 "insect larva" means that the birds were carrying a single large larva in each visit, while "insect larvae" means that they were carrying many small larvae. The predominant food items were wood roaches (Blattidae) in the genus *Parcoblatta*, which were present in 69.4% of the visits with recognizable prey. Other common prey items were wood-borer larvae (Cerambycidae or Bupres-

TABLE 1

TOTAL VISITS OF 12 ADULT RED-COCKADED WOODPECKERS WITH ARTHROPOD PREY TO FOUR NEST CAVITIES ON THE SAVANNAH RIVER SITE

Prey item	Number of observations	Percent of visits
Wood roach (*Parcoblatta* sp.)	1310	69.4
Wood borer beetle (larva) (Cerambycidae or Buprestidae)	103	5.4
Moth (larva) (Lepidoptera)	85	4.5
Spider (Araneae)	68	3.6
Ant (larvae and adults) (Formicidae)	58	3.1
Longhorned grasshopper (*Atlanticus* sp.)	55	2.9
Centipede (Scolopendromorpha)	53	2.8
Insect (larva) (Insecta)	49	2.6
Insect (larvae) (Insecta)	38	2.0
Beetle (larva) (Coleoptera)	15	0.8
Moth or butterfly (pupa) (Lepidoptera)	11	0.6
Beetle (pupa) (Coleoptera)	6	0.3
Wasp or bee (larva) (Hymenoptera)	4	0.2
Wood roach (ootheca) (Blattidae)	4	0.1
Wood borer (pupa) (Cerambycidae or Buprestidae)	3	0.1
Insect (pupa) (Insecta)	2	0.1
Wasp (adult) (Hymenoptera)	2	0.1
Weevil (adult) (Curculionidae)	2	0.1
Cicada (adult) (Cicadidae)	2	0.1
Short-horned grasshopper (Acrididae)	1	<0.1
Metallic wood boring beetle (adult) (Buprestidae)	1	<0.1

TABLE 1
CONTINUED

Prey item	Number of observations	Percent of visits
Long-horned beetle (adult) (Cerambycidae)	1	<0.1
Fly (adult) (Diptera)	1	<0.1
Click beetle (adult) (Elateridae)	1	<0.1
Cricket (Gryllidae)	1	<0.1
Stonefly (adult) (Plecoptera)	1	<0.1
Silverfish (Lepismatidae)	1	<0.1
Homoptera (nymphs)	1	<0.1

tidae), moth larvae (Lepidoptera), spiders (Araneae), ants (Formicidae), long-horned grasshoppers (Tettigoniidae) in the genus *Atlanticus*, and centipedes (Chilopoda).

We photographed birds feeding both *Crematogaster* sp. and *Camponotus* sp. ants to nestlings, but the majority of our records were of *Camponotus* sp., possibly because they were larger and easier to recognize. In our study, many bird visits with ants were assigned to the "insect larvae" category unless we could identify a recognizable adult among the larvae. In fact, we suspect that this category is primarily composed of visits with ants. Each visit involving ants always included a number of individuals (primarily larvae). Although we were unable to count the number of ants present during each visit, a conservative estimate would be five per visit which would make ants the second most abundant prey item in our study. It is unclear whether they are as important as the numerical data suggest because of their small size. However, some insight might be gained by comparison of oven-dried mass of ants and roaches (Hanula and Franzreb, unpubl. data). The average (N = 596) dry mass of a *Camponotus* spp. ant adult is 0.00418 g or 0.0209 g for five individuals. The average (N = 660) mass of a wood roach is 0.01376 g. Therefore, the estimated total biomass of roaches observed during our study was 18.03 g and that of ants (assuming 5 ants/visit) was 2.01 g.

Roaches were the only prey that were consistently taken by all of the woodpecker groups (Table 2). Other prey listed in Tables 1 and 2 were frequently collected in large numbers only by a single group. For ex-

TABLE 2
DIFFERENCES IN PROPORTION OF THE 10 MOST COMMON ARTHROPOD PREY AMONG WOODPECKER GROUPS

Prey	Percent of total visits with prey			
	Group 3	Group 18	Group 19	Group 39
Wood roach (*Parcoblatta* sp.)	69.8	63.3	81.6	72.2
Wood borer beetle (larva) (Cerambycidae or Buprestidae)	12.6	1.6	0.0	1.8
Moth (larva) (Lepidoptera)	1.6	9.4	1.9	2.8
Spider (Araneae)	2.3	5.4	2.9	3.0
Ant (larvae and adults) (Formicidae)	3.0	0.2	1.0	7.1
Longhorned grasshopper (*Atlanticus* sp.)	0.0	8.8	0.0	0.0
Centipede (Scolopendromorpha)	1.2	3.7	2.9	3.6
Insect (larva) (Insecta)	2.6	2.8	3.9	2.2
Insect (larvae) (Insecta)	3.0	0.5	0.0	3.0
Beetle (larva) (Coeloptera)	0.8	1.0	0.0	0.8

ample, wood-borer larvae were the second most abundant prey item overall (Table 1). The majority of these were taken by woodpeckers in Group 3 where they made up 12.6% of the visits, while they made up less than 2% of the visits in each of the other groups (Table 2). Similarly, longhorned grasshoppers were utilized only by birds in Group 18. The 55 grasshoppers we observed on the slides were all collected by one bird.

We compared the number of the various prey brought to the nest cavity to the age of the nestlings in the cavity and found no difference in the type of prey fed to young nestlings (e.g., 5–6 days old) versus that fed to older nestlings (e.g., 19–20 days old). Roaches made up the bulk of the diet of nestlings regardless of age. However, we did not have observations for nestlings younger than five days old.

Helper males made fewer visits than either the breeding males or the breeding females (Table 3). For example, the two helper males in Group 19 each made ca. 19% of the visits compared to 35.7% and 26.7% for the breeding male and female, respectively. Breeding females made fewer visits than the breeding males in the three groups with helper males, but

TABLE 3
PROPORTION OF FEEDING VISITS BY RED-COCKADED WOODPECKER BREEDING PAIRS AND HELPER MALES

Group	Bird status	Number of visits	Percent of total visits
3	Breeding male	458	46.2
	Breeding female	378	38.1
	Helper male	156	15.7
19	Breeding male	75	35.7
	Breeding female	56	26.7
	Helper male 1	40	19.0
	Helper male 2	39	18.6
39	Breeding male	341	43.4
	Breeding female	249	31.8
	Helper male	196	24.9
18	Breeding male	400	44.3
	Breeding female	502	55.5

they made more visits than the breeding males in the group that had no helper males.

DISCUSSION

The few studies of prey of Red-cockaded Woodpeckers suggest that they are generalists taking advantage of available arthropods. For example, Red-cockaded Woodpeckers have frequently been reported foraging in corn fields (Ward 1930, Ligon 1970, Baker 1971) where they feed on corn earworms (*Heliothis zea*) and corn leaf aphids (*Rhopalosiphum maidis*) (Baker 1971). Beal (1911) and Beal et al. (1916) analyzed the gut contents of 99 Red-cockaded Woodpeckers taken throughout the year. They reported that ants in the genera *Camponotus* and *Crematogaster* were the most common prey of adult birds, based on numerical counts, but they did not tell which genus was more prevalent or how the birds were collected and handled following collection.

More recent studies have shown that gut content analysis of birds can have limitations resulting from differential rates of prey digestion (Rosenberg and Cooper 1990). For example, Koersvald (1951) showed that in Corvidae the digestion of food continues for some time after bird death. Dillery (1965) compared the content of stomachs of Savannah Sparrows (*Passerculus sandwichensis*) preserved immediately after collection to specimens that received no preservation treatment. He concluded that the results of analysis on stomach contents where digestion was not stopped

can be biased, since hard to digest parts "are like gravel" and can remain in the stomach for sometime, while more easily digested material can disappear within five minutes. Other studies have demonstrated that the digestion rates of arthropods vary among prey items, bird species, and state of bird starvation (Custer and Pitelka 1975, Gartshore et al. 1979, Coleman 1974, Stevenson 1933, Mook and Marshall 1965). Mook and Marshall (1965) concluded that, without a knowledge of the digestion time and the digestion rate of arthropod prey in a given species of bird, it is not possible to use gizzard analysis in a quantitative way. Thus, information on the prey of Red-cockaded Woodpeckers based on stomach analysis (Beal 1911, Beal et al. 1916) probably should be consider qualitative.

Both *Crematogaster* sp. and *Camponotus* sp. construct nests in live trees. We frequently observed *Crematogaster* sp. nesting in the thick outer bark (and occasionally in dead limbs), while *Camponotus* sp. were found nesting in dead branches in the crown of live trees. Although *Camponotus* sp. also nest in dead trees, it is the nests in live trees where they are most likely to be encountered by Red-cockaded Woodpeckers. Ants were the second most abundant prey numerically when one considers that each visit to the nest with ants was with a number of individuals. However, comparison of the biomass of ants and roaches shows that the rankings based on numbers of visits (Tables 1 and 2) provides a relatively accurate picture of the overall value of each group of prey in the diet of the Red-cockaded Woodpecker.

Beal (1911) and Beal et al. (1916) reported that Coleoptera larvae, primarily of wood boring beetles, were found in the stomachs of adult Red-cockaded Woodpeckers. Harlow and Lennartz (1977) grouped all insect larvae into one category, which was their most commonly recorded prey item. Although it is impossible to know which larvae they observed, it is interesting to note that their study site was located on the Francis Marion National Forest, which Price et al. (1991) reported suffering an outbreak of southern pine beetles (*Dendroctonus frontalis*) from 1971 and through 1976 the year of their woodpecker prey study. Therefore, it is likely that woodpeckers had access to an abundance of wood-boring larvae commonly found associated with bark beetle-killed trees.

We found wood borer larvae of the families Cerambycidae or Buprestidae to be the second most abundant prey item overall at the Savannah River Site. These are large insects (3–6 cm long) whose audible feeding makes them relatively easy to find. We did not observe Red-cockaded Woodpeckers removing large amounts of loose bark from dead and dying trees, suggesting that they were not foraging for bark beetles (Scolytidae) or other common insects associated with recently killed trees but that they

were foraging specifically for the wood borer larvae. However, the insects we recorded as "Coleoptera larva," "Coleoptera pupa," and most of the "insect larva" records were likely taken from dying or dead trees or from the dead limbs of live trees, since insect larvae rarely occur in the outer bark of live trees (Hanula and Franzreb, unpubl. data). Table 2 shows that wood borer larvae were important only when they were locally abundant, as they were for Group 3 whose nest cavity was within 200 m of a small cluster of bark beetle-killed trees. Wood borers ranked no higher than seventh in numerical abundance of prey for the other three clusters.

Beal (1911) and Beal et al. (1916) found roaches in adult Red-cockaded Woodpeckers but only in the form of ootheca (egg cases). Conversely, Harlow and Lennartz (1977) reported roaches as the third most abundant item in the diet of nestlings after insect larvae and centipedes. In our study, roaches were present in most of the nest visits. Like many insects, their population may periodically increase followed by periods of scarcity. Whether 1993 was a year of relative roach abundance on our study areas is unknown, but fluctuations in populations may explain why the relative importance of this prey item varies among the studies.

Red-cockaded Woodpeckers used a number of Lepidoptera larvae that we were not able to identify. However, we did photograph five visits in which the adults were carrying coneworm larvae (*Dioryctria* sp.), which are borers found in the cones of several southern softwood species. Hooper and Lennartz (1981) observed both sexes pecking green pine cones and speculated that they were extracting coneworms.

When helper males were present, females made fewer visits than the breeding males. In this respect, our results are consistent with those of Lennartz and Harlow (1979) who found that in five Red-cockaded Woodpeckers groups on the Francis Marion National Forest, breeding males tended to make more visits to feed nestlings than females, regardless of the presence of helpers. They found that when helpers were present, breeding males averaged only 30% of the visits, while breeding females averaged 27%. Males made an average of 59% of the visits and females 41% for three pairs with helpers. Females never contributed more than 50% of the visits. Conversely, in our one instance of a pair without helpers, the female fed the young substantially more often than her mate (55% vs 44%).

Our study demonstrates the feasibility of using still photography for studying Red-cockaded Woodpecker prey selection during the nesting season. It is the first study on this bird to compare the diets of young in individual clusters. Although still photography is not a new technique for studying bird diets (Rosenberg and Cooper 1990), it proved more effective than a comparably priced video camera system (Franzreb and Hanula

1995) or personal observation (Harlow and Lennartz 1977), and the cameras had no observable impact on the adults or nestlings we photographed.

ACKNOWLEDGMENTS

We thank D. White, K. Laves, M. Stacklin, T. Kuntz, and H. Barnhill, for technical assistance, and D. Dwinell (USFS), D. Hamrick, and J. Strawser (Univ. of Georgia, CES) for helpful discussions during the development of the camera system. We also thank R. Conner, T. Sherry, and W. Tschinkel for helpful comments on an early draft of this manuscript. This project was supported by the Dept. of Energy, Savannah River Site, and the USDA Forest Service, Savannah River Forest Station. The mention of trade names in this paper is for the information and convenience of the reader. Such use does not constitute official endorsement or approval by the U.S. Dept. of Agriculture of any product to the exclusion of other products that may be available.

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THE CALLS AND ASSOCIATED BEHAVIOR OF BREEDING WILLOW PTARMIGAN IN CANADA

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ABSTRACT.—We describe the physical structure, use, and possible functions of 11 calls of breeding Willow Ptarmigan (*Lagopus lagopus*), most of which were given by both sexes. Both sexes had visually and acoustically conspicuous territorial calls (flight song, rattle, "kohwa," and "aroo" (males only). "Koks," "ko-ko-ko," and "krrow" were given by both sexes as low intensity threat, territorial, or sexual situations, or to maintain contact with the mate or offspring. "Purr" and "moan" were given usually by females to communicate with chicks, and "hiss" and "scream" calls by both sexes in intense defence of offspring or mates. The sex of the caller was usually easily recognizable, as males had strong and rapid amplitude modulations in their calls, which females lacked. The most complex calls were flight songs which consisted of several calls in sequence. Unlike other nonpasserines, Willow Ptarmigan do not appear to have a repertoire of calls that are graded variants of one another. Calls of North American populations of Willow Ptarmigan appear similar to those of European populations. *Received 2 June 1994, 5 Mar. 1995.*

The social systems of grouse (Phasianidae: Tetraoninae) have been well studied (Hjorth 1970, 1976, Wiley 1974, Wittenberger 1978, Johnsgard 1983), but their vocal repertoires are poorly described, with few complete vocal ethograms that include sonograms for both sexes, but see Stirling and Bendell (1970). Ptarmigan are particularly interesting because they are one of the few monogamous members of the subfamily Tetraoninae. Willow Ptarmigan (*Lagopus lagopus*) males provide parental care, and after the eggs hatch, they can raise young on their own (Wittenberger 1978, Martin and Cooke 1987). Thus, members of Willow Ptarmigan pairs and broods are in frequent vocal contact during the breeding season. Qualitative descriptions of the calls of Red Grouse (*L. l. scoticus*) in Scotland have been reported by Watson and Jenkins (1964). Cramp and Simmons (1980) provided sonograms for several of these calls. In Norway, several territorial and mating calls of free-living birds of the continental European subspecies (*L. l. lagopus*) are described (Pedersen et al. 1983, Johnsen et al. 1991), and Wike and Steen (1987) described four parental calls, three with accompanying sonograms of three captive brood hens. The calls of North American Willow Ptarmigan have not been described. In this paper we describe the calls of free-living breeding birds in northern Canada and provide details on the context of their use.

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METHODS

Calls of Willow Ptarmigan were recorded at two sites in northern Canada: a population of *L. l. albus* (Johnsgard 1983) at La Perouse Bay (LPB) (58°24′N, 94°24′W), 40 km east of Churchill, Manitoba (Martin 1984) and a population of *L. l. alexandrae* (Johnsgard 1983), 2500 km west of LPB, at Chilkat Pass (CP) in northwestern British Columbia (59°50′N, 136°30′W) (Hannon 1983, 1984). The general biology, behavioral ecology, and life history of both of these Willow Ptarmigan populations have been documented elsewhere (Hannon 1983, 1984, Martin 1984, Martin and Cooke 1987, Martin et al. 1989, Hannon and Martin 1992, Mossop 1988). At both sites, males arrived on territories in mid- to late April, shortly before females. Nests were visited every 2–4 days until hatch or clutch failure (Hannon et al. 1993). During the breeding season most individuals can be approached within 10 m and less than 3 m for birds with nests and broods. Pairs remain together until mid-August or through September.

At LPB, we conducted 49 recording sessions of one or both members of 17 pairs (13 males, 16 females) during 18 Jun.–4 July 1984. Color-marked individuals were recorded one to four times. We described the behavior accompanying the vocalization and the response of the mate, the offspring, or neighboring birds to the individual vocalizing at each session. To establish further the behavioral context of parental vocalizations, we conducted watches at 22 nests from blinds placed 8–10 m away during late incubation and the first day of brooding in 1982 and 1983. During the breeding seasons of 1981–84, we made opportunistic observations of vocalizations and contextual behavior from mid-April to mid-August. As a consequence of female removal experiments at hatch (Martin 1987, Martin and Cooke 1987), we were able to obtain recordings of a range of male parental calls that would not be readily observed in bi-parental pairs. At CP, both sexes of ptarmigan were recorded during territorial establishment in late April and early May 1980, 1981, and 1986. By combining recordings from both sites, we assembled a comprehensive vocal repertoire for both sexes of Willow Ptarmigan during the breeding season. Where possible, we used the descriptions of Watson and Jenkins (1964) as a reference.

Initial categorization of calls was by ear during fieldwork by KM (LPB) and SJH (CP). In the laboratory, AGH listened to the field tapes and analyzed at least one example of each category of call (one or a series of notes) encountered for each individual. Calls were considered to belong to different categories if the difference between them was qualitative rather than quantitative. Thus, categories differed in whether they were frequency modulated or not, had one note or not, etc. An over-estimate of the number of call categories would result from this method if, for example, a particular individual had an aberrant call or if intermediates between call types were missed. We are confident this did not occur in our study. However, we may have under-estimated the number of categories because we pooled calls that could have been distinguished using quantitative measures of their acoustic characteristics. Although it is possible that our tape machine missed all or parts of calls, we were able to tape very low amplitude calls such as quiet "moans" (see Fig. 4B).

Vocalizations were digitized using SoundWave software at nine bits and a sampling rate of 22 kHz. The resulting files were converted to 12-bit files and analysed using MacSpeech Lab II software. For purposes of illustration, we selected clean recordings that gave a range of variation in the calls or that clearly showed the typical features of the call type. These were produced using Canary 1.1 software at a filter bandwidth of 705 Hz, analysis bandwidth of 173 Hz, and a time resolution of 1.4 ms.

RESULTS

Koks.—"Kok"s were short (about 50 ms) calls that were strongly sexually dimorphic (Fig. 1A, B). In males, calls showed rapid amplitude

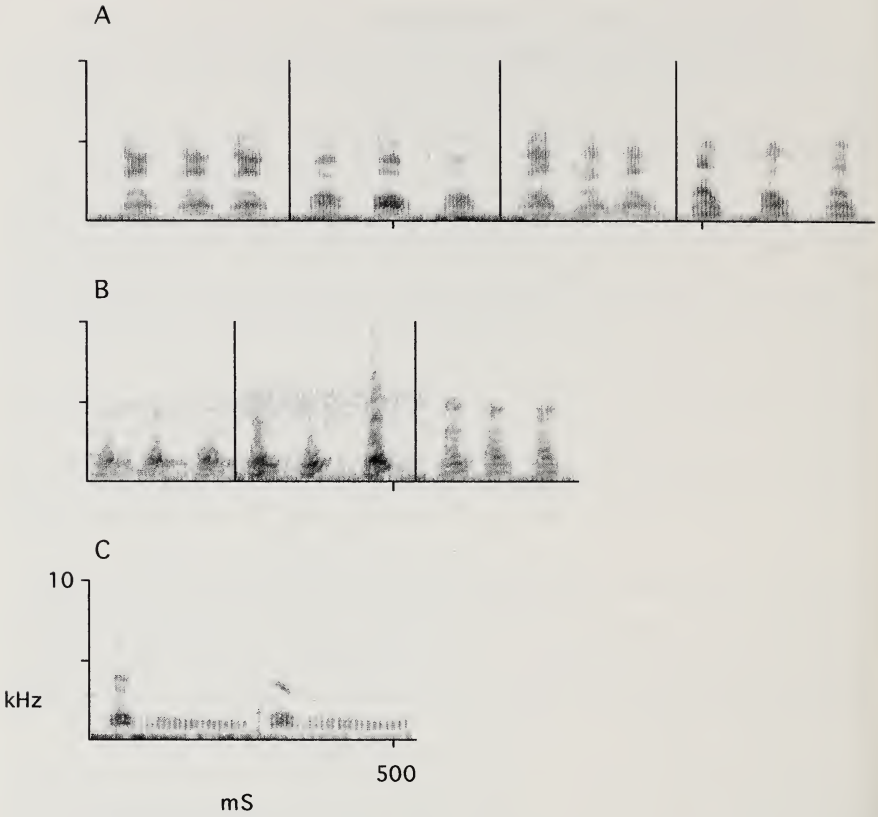

FIG. 1. Willow Ptarmigan: A—three "kok"s from each of four males; B—three "kok"s from each of three females; C—two "ko-ko-ko"s from one male. Vertical lines separate individuals. Note differences between as opposed to within individuals in both A and B.

modulation (pattern of loud and soft sounds) with a fundamental frequency that usually remained around 1000 Hz and that had a sharp onset and termination, showing sidebands that appeared to be formants (broad horizontal bars, sometimes indistinct) rather than harmonics (equidistant horizontal bars, generally narrow). In females, they were less strongly amplitude-modulated and showed two to six distinct harmonics. The frequency modulation of the calls were downward, upward, or up and down (chevron-shaped), depending on the individual and possibly on the situation. The abruptness and rapid amplitude modulation of male "kok"s (Fig. 1A) made them sound like "bek"; the smoother envelope (overall pattern of loudness) of female "kok"s (Fig. 1B) made them sound like variants on "cluck."

"Kok"s were given in prolonged bouts while paired birds were foraging near one another, during territorial and sexual interactions, and when intruders (predators or humans) were close to nests or broods. We observed more intra-individual variation in female "kok"s than in males (Fig. 1A, B). This call may indicate general arousal, as they were used both as contact calls and to indicate the presence of a potential threat. The rate of delivery varied from about 20 to 120 per minute. The rate of delivery and the abruptness of their onset and termination may be a graded signal of the intensity of the arousal (e.g., with the approach of a predator). Watson and Jenkins (1964) noted that amplitude, sharpness of onset and termination, and rate of delivery appeared to increase with speed of aerial chases and with intensity of response to a predator at the nest. They classified the variation in the structure of this call into two categories, "chase kok"s and "warning kok"s. More detailed analyses of our populations might support such divisions.

Ko-ko-ko.—This was a low amplitude call given in prolonged bouts, often with several "ko" notes strung together (Fig. 1C). They had a relatively low fundamental frequency (below 1000 Hz) and were rapidly amplitude-modulated, basically making them low growls or "purr"s. "Ko-ko-ko" calls were given by males in low level alert postures and were not specifically associated with any one behavior. Watson and Jenkins (1964) suggested that they were flight intention calls. They may be homologous to female "purr"s.

Krrow.—These were medium length (50–300 ms) calls that rose quickly and fell slowly in frequency (Fig. 2A, B). In males, they were rapidly amplitude-modulated with a fundamental frequency of about 1500 Hz that varied by about 30 Hz throughout the call (Fig. 2A). Two to three formants were present in males; a shift in their emphasis to higher frequencies about one-third through the call made them sound like "bugow". In females, the initial rise in frequency was more abrupt, and several harmonics were apparent, making the call sound like "meow" (Fig. 2B). "Krrow"s were sometimes given singly but were usually in bouts of two to five calls.

"Krrow"s were frequent during intra-sexual territorial encounters, during which calls were exchanged rapidly between neighboring males or females along with "kohwa"s (especially between males). "Krrow"s were also used to regain contact with mates and young. Females gave "krrow"s after their mate left them temporarily during the pre-incubation period in eight out of nine cases at LPB in which females vocalized; these calls stopped when the male returned. At CP, males frequently flew to their mates when females gave "krrow"s. During brood rearing, they were usually given by the parent to dispersed chicks. The calling bird uttered

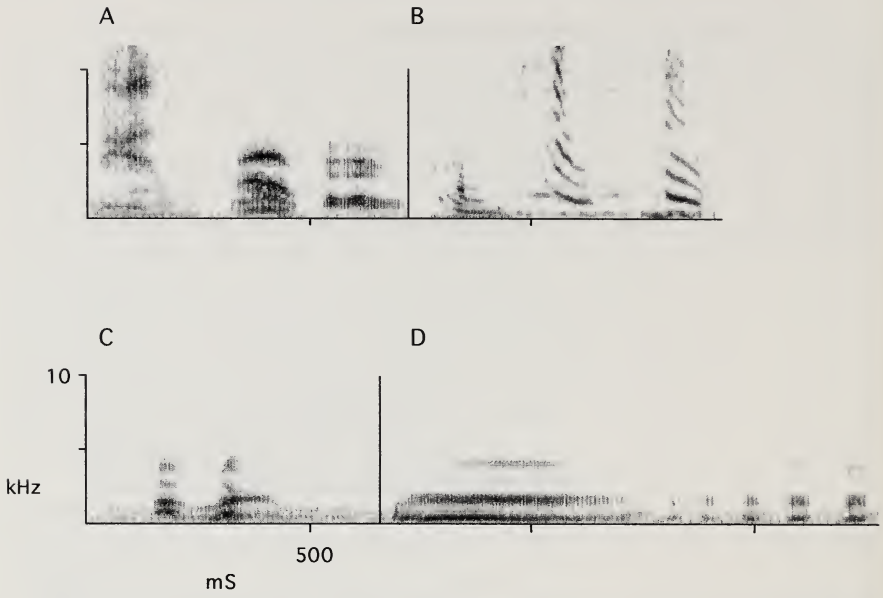

FIG. 2. Willow Ptarmigan: A—"krrow"s of three males; B—"krrow"s of three females; C—"aroo"; D—the next "aroo" given by the same male, trailing off into a "rattle".

"krrow"s at a rate of 2–30 per minute until all the chicks had gathered, after which the calls stopped abruptly. Watson and Jenkins (1964) described the "krrow" as a threat and contact call used for intra-sexual aggression and for establishing or maintaining contact within pairs and with young. Johnsen et al. (1991) referred to the "krrow" as a "weak threat" call but also indicated that Norwegian Willow Ptarmigan used this call in social and sexual situations.

Kohwa.—"Kohwa"s were amplitude-modulated, medium length (about 100 ms) calls with a distinctive overall pattern of frequency modulation—a brief up and down followed by a longer up and down pattern and a flat terminal portion, changing by about 500 Hz (call shown in latter half of Fig. 3C).

"Kohwa"s were most commonly given in territorial encounters, when rapid bouts of calls were exchanged between males in alternation with rapid bouts of "krrow"s. In these bouts they were sometimes given in a series and sounded like "gowayogowayo . . ." They also formed the terminal portion of flight songs (Fig. 3C) and were given during strong responses to disturbance by intruders at nests (Martin 1985, Hik et al. 1986). Females occasionally gave this call at CP during border disputes. "Kohwa"s given singly or in strings did not differ enough to qualify as

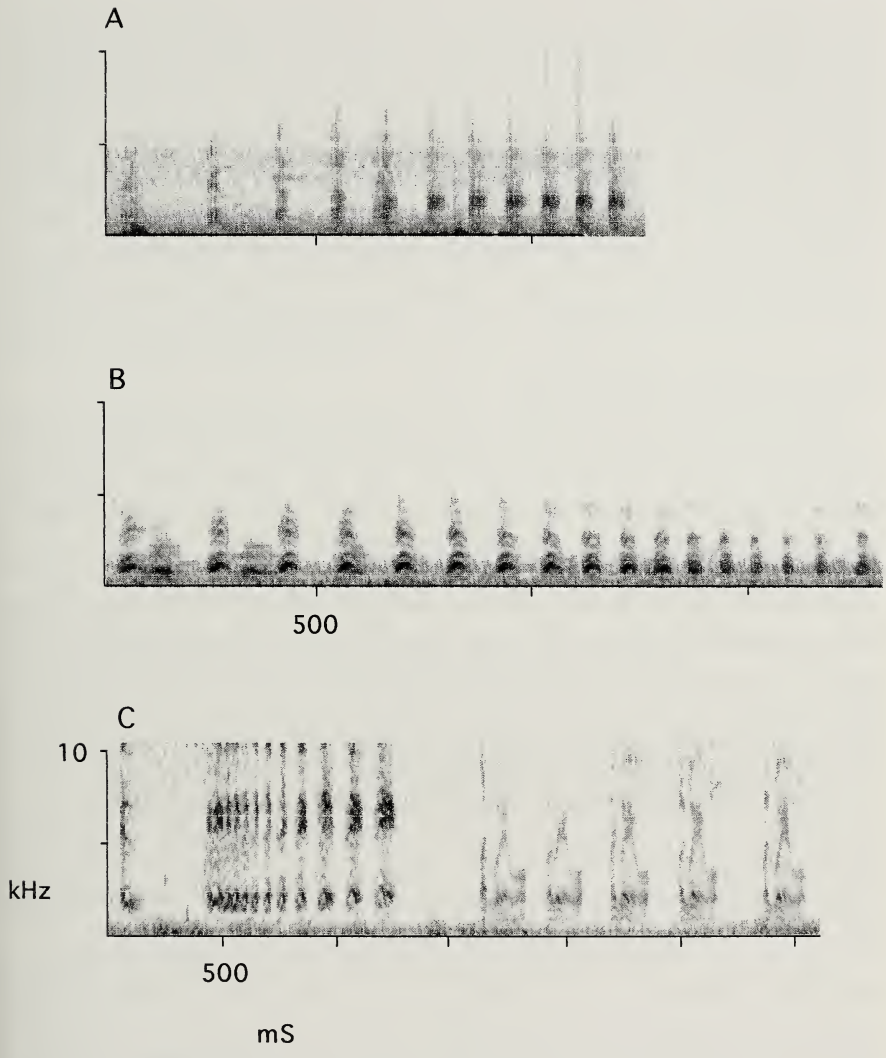

FIG. 3. Willow Ptarmigan: A—"rattle" of a male; B—"rattle" of a female; C—"flight song" of a male.

separate categories by our criteria, and they occurred too infrequently during the nesting period for us to determine differences in their use. In European populations, "kohwa" and "kohway" calls are described as attack and attack intention calls (Watson and Jenkins 1964, Johnsen et al. 1991).

Aroo.—"Aroo" was a highly variable call, with an overall falling and

rising pattern of frequency modulation and rapid amplitude modulation at a varying rate and intensity (Fig. 2C, D). An initial medium-length (500 ms) note was usually followed by shorter notes with indeterminant structure, usually similar to the initial note but chevron-shaped. "Aroo"s sometimes formed a graded series with "kohwa"s and were combined with other calls (e.g., "rattle"s, Fig. 2D) during intense territorial encounters.

Observations early in the breeding season at LPB suggested "aroo"s were given by males in the most intense territorial disputes and frequently preceded physical aggression. "Aroo"s occurred less frequently during the nesting period but again were associated with intense defense of offspring by males (Martin 1987).

Rattle (song on the ground).—The rattle was a long accelerating string (800 ms) of short elements that were quite similar to "kok"s and may be modified versions of them (Fig. 3A, B). As in other calls, elements showed rapid amplitude-modulation in males (Fig. 3A), giving them a harsher quality than calls of females (Fig. 3B).

Both sexes gave "rattle"s spontaneously or in response to the "rattle" of another male or to "krrow"s by females. "Rattle"s were one of the more common male calls for low intensity territorial advertisement and defence, especially in early spring and at dawn later in the breeding season. Females at CP gave "rattle"s fairly commonly at dawn in early spring shortly after they arrived on territory, often in response to hearing or seeing another female on their territory.

"Rattle"s were also given when intruders entered a territory, approached a nest, or when one of the pair was flushed by an observer. In such instances, they were almost always preceded by high rates of "kok"s. The association with accelerating bouts of "kok"s, suggested that the "rattle" was given during an increased state of arousal.

Flight song.—The vocalization given during territorial flight displays was a two-part series of calls (Fig. 3C). The first part was a decelerating series of what appears to be modified "ko-ko-ko"s and the second consisted of "kohwa"s. The notes in the first section of the flight song were chevrons with a peak frequency of 2000–2500 Hz and length of 26–31 ms. The first and second note in the first part of the flight song were separated by a pause, the next two to four notes ran together, and the following six or more notes decelerated and lengthened. The second part of the flight display consisted of decelerating "kohwa"s.

Flight songs occured in several situations. They were given by both sexes during territorial advertisement, most frequently at dawn or after territorial encounters. Flight songs by one individual often stimulated flight displays among neighbors, in a manner similar to the songs of many

passerines. Abbreviated flight songs, without "kohwa" elements, were frequently given when males were disturbed from resting or hiding sites. Flight displays also occurred when males rejoined their mates after a brief absence and during nest defense, particularly upon the return of the male to the nest site. During forced choice experiments, many males at LPB preferentially defended their female rather than their eggs during early incubation (Martin 1984). In these tests, males that chose to defend their mates gave flight songs, but males that defended their offspring did not (KM, unpubl. data). At CP, females gave flight songs in early spring when they heard or saw another female on their territory. This behavior ceased when egg laying commenced.

Flight songs were the most complex of the ptarmigan calls we measured. When given spontaneously, they appeared to correspond in function to the songs of other bird species, notably shorebirds and passerines, in broadcasting information about territory ownership, and without being directed to specific individuals or associated with specific interactional behaviors. When used upon returning to the mate, they may function in the same capacity as greeting ceremonies in Anseriformes and Psittaciformes. As in these analogous behaviors, the complexity of the call may identify the individual, but their complexity seems excessive for this function alone and may indicate the singer's quality as well.

Purrs.—Heard only from females, "purr"s were short, low frequency (c. 800 Hz), irregular trains of pulses (loud part of note) that rose and then fell in frequency over about 50 Hz (Fig. 4A). They varied greatly in amplitude but without obvious changes in the details of their structure. During a disturbance at the nest, "purr"s were given in similar situations to "kok"s and usually when "kok" rates were high. In this situation, a "purr" appeared to be an alarm call of higher intensity than a "kok" but lower than a "hiss". "Purr"s were also given when females returned to their nests after an incubation recess or after being flushed from the nest during incubation and hence may advertise attachment to the nest site.

Moan.—"Moan"s are low frequency, medium length calls with relatively few harmonics and, unlike most ptarmigan calls, lack amplitude modulation (Fig. 4B). "Moan"s were heard mainly from females and were given singly or in bouts, sometimes being introduced without pause by a "kok", making a "kok-moan." "Moan"s were given when females gathered their chicks for brooding or moved them away from the site of a disturbance. This call appeared to function as a "come hither" command since young chicks responded immediately to the "moan" by approaching and following the female. When we imitated the "moan", chicks less than five days of age emerged from cover and approached us,

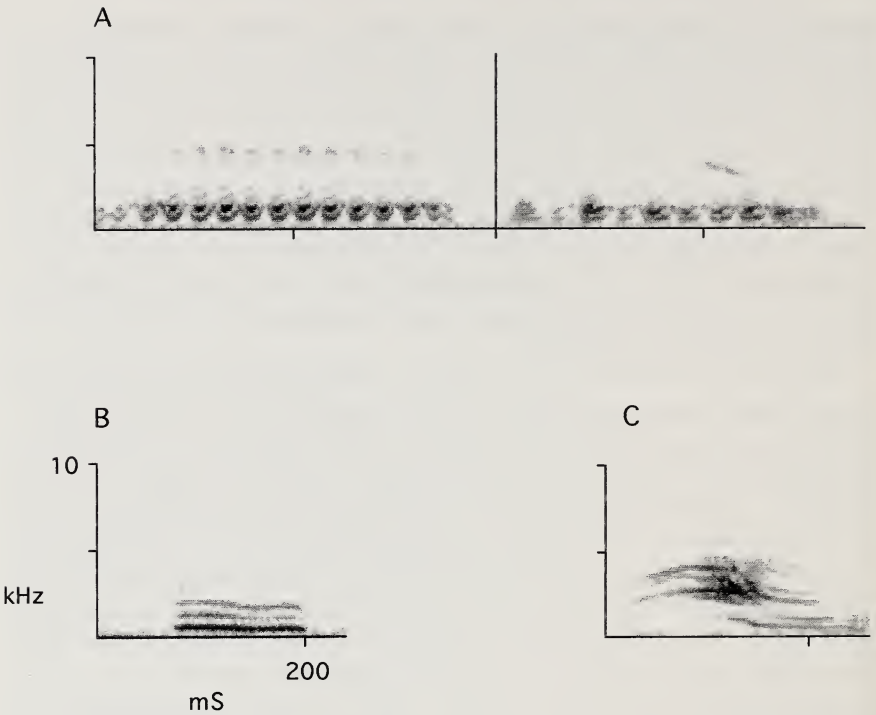

FIG. 4. Willow Ptarmigan: A—"purr" of two females; B—"moan" of a female; C—"scream" of a female. Vertical lines separate individuals.

sometimes walking over our feet or legs or our bird dogs to approach the calls. Older chicks moved from their hiding place but stopped when they saw us. We lacked a sufficient sample of females to examine individual variation in the "moan", but Allen et al. (1977) indicated that chicks recognized their mothers' call. We observed little mixing of wing-tagged chicks between broods in either population. Possibly, the "moan" assists in brood cohesion as well as a call to gather.

Scream.—This was a noisy call with an indeterminate harmonic structure, a relatively high fundamental frequency, and given in brief, loud bouts (Fig. 4C). "Scream"s were given in distress situations when females were suddenly flushed from the nest and by both sexes during intense defense of nests or broods. A male single parent gave "scream"s as he attacked a female Northern Harrier (*Circus cyaneus*) that approached his brood of 10 two-day-old chicks (Martin 1987).

Hiss.—A "hiss" (not illustrated) was a band of white noise about 2 s long and was given during distraction displays. Parents of both sexes were

observed to "hiss" when disturbed at the nest or with young chicks. Occasionally, adults and chicks several weeks old "hiss"ed when being held by observers.

DISCUSSION

The vocal repertoire of Willow Ptarmigan in North America consists of at least 11 calls, most of which are given by both sexes and in both populations. We did not attempt to compare the calls or the context between our two populations because of our limited sample of many calls and because the emphasis in our respective studies differed, resulting in different opportunities to record various calls and to observe the contextual behavior. For example, female "rattle"s were heard more frequently at CP than at LPB, perhaps because the density of birds was higher at CP (Hannon et al. 1988) or possibly because there was more emphasis on territorial behavior, especially of females, in the CP study (Hannon 1983, 1984) compared to the LPB study. Most parental calls for both sexes were recorded at LPB, given the emphasis on parental behavior in this study (Martin 1987, Martin and Cooke 1987).

In several cases, call types such as "purr", "moan" and "aroo" were given predominantly by one sex. In some instances, this may relate to the opportunities to record such calls. For example, during brood rearing females do most of the vocal communication to young chicks. We were able to sample the repertoire of male parental calls more completely in our study as a consequence of experiments at LPB where we removed female parents on the day of hatch (Martin 1987, Martin and Cooke 1987). During watches, we heard single parent males use modified (lower and softer) "kok"s, "krrow"s, and "ko-ko-ko"s to communicate with their day-old chicks, but we did not hear them give calls equivalent to the "moan" or "purr". However, all watches were done within several hours of the hen removal, and it is possible that single parent males developed these brood contact calls later. Most single parent males successfully raised several of their offspring (Martin and Cooke 1987).

We observed several additional calls that we were unable to record. There were calls to warn of the approach of avian or mammalian predators; the response of the mate or chick is to freeze or to run for cover and then crouch. At both sites, we heard birds give separate calls to warn of approaching avian and mammalian predators. Watson and Jenkins (1964) described the avian predator call as a "chorrow," and they observed birds giving a loud and high pitched "kok" to warn of approaching mammalian predators. We have not observed females give food calls to attract chicks to food sources at either LPB or CP, but these likely exist. In captivity, a two-syllable food call ("ku-ku"), similar to the "tid-

bitting" food call used by domestic poultry, was given by Willow Ptarmigan brood hens in Norway (Wike and Steen 1987), and Scottish Red Grouse chicks responded to the food calls of domestic poultry foster parents (Watson and Jenkins 1964). Food calls have been observed for wild North American White-tailed Ptarmigan (*L. leucurus*) (Braun et al. 1993).

Several ptarmigan vocalizations appear specialized for reunion of family members and for crisis situations such as predator intrusions. Individuality in "kok"s and "krrow"s, for example, was apparent both on sonograms and to our ears, although our data set precluded a detailed analysis of this. Most calls showed relatively sharp onsets and wide frequency ranges, features that should make them easy to locate. The "moan", "ko-ko-ko", and "purr" were exceptions to this rule and were often given at low amplitude when the caller's apparent intent was to remain cryptic.

Most Willow Ptarmigan calls were strongly sexually dimorphic, even to our ears. Male calls were consistently strongly amplitude-modulated, and their calls generally showed formants rather than the harmonics seen in female calls, suggesting that the sexes produce their calls differently. From a functional perspective, males may give more abrupt, broad spectrum calls that are easier to locate (Marler 1955) than females in the presence of predators because males wish to lead predators from the vicinity of their nests or broods (Hannon and Martin 1992).

Most grouse species show little parental care by males and large sexual dimorphisms in plumage and displays (Wiley 1974). Willow Ptarmigan deviate from this general pattern by showing extensive male care (Martin and Cooke 1987) and less sexual dimorphism. Sexual dimorphism in calls is also less pronounced for Willow Ptarmigan than for other grouse species (Cramp and Simmons 1980, Johnsgard 1983). Willow Ptarmigan form long term pair bonds, and thus male calls serve territorial, sexual, social, and parental functions. Also, female Willow Ptarmigan are territorial and show intra-sexual aggression (Hannon 1983, Martin et al. 1990). The monogamous bi-parental mating system of Willow Ptarmigan results in the need for members of pairs to communicate with each other and their offspring thoughout the breeding season. This may explain the almost complete sharing of calls by both sexes of Willow Ptarmigan compared to other members of the Tetraoninae.

Different observers might classify calls differently, thus making the absolute repertoire size of a species difficult to compare with that of other groups or populations. Also, there is the additional complication of asymmetric opportunities to sample calls equivalently for both sexes and throughout the breeding season. However, our classification for Willow

Ptarmigan broadly agrees with that of Watson and Jenkins (1964). Except for the "kohwa-aroo" series of calls, we found no obvious intermediates between the call types we described, unlike the majority of other studies of calls in nonpasserines (e.g., Jenni et al. 1974, Huxley and Wilkinson 1977, Clapperton and Jenkins 1984, Collias 1987). If our estimate of repertoire size is correct, Willow Ptarmigan have a mid-sized repertoire compared to other nonpasserines. Compared to other Tetraoninae, ptarmigan have the largest repertoire of calls, and Willow Ptarmigan appear to have the greatest amount of overlap of calls used by both sexes (Cramp and Simmons 1980, Johnsgard 1983).

Willow Ptarmigan are an excellent species to conduct detailed studies of vocalizations in relation to the behavior, genetics, and life history of individuals since they are easy to approach, record, and observe. Multiple recording sessions of individuals are possible, and most individuals and their relatives in a population can be sampled. High male natal philopatry (Martin and Hannon 1987) would allow examination of the heritability of calls such as "kohwa," "kok," "ko-ko-ko," "krrow," "aroo," "rattle," and "flight song." Finally, variation in calls could be examined in relation to mate choice, social behaviors, and life history consequences.

ACKNOWLEDGMENTS

We thank S. Stevenson and S. Alexander, for assistance in behavioral observations at LPB, and J. S. Schieck for assistance in recording birds at CP. This study was funded by Natural Sciences and Engineering Research Council (CANADA) grants to KM, SH, and F. Cooke, and funds from the Univ. of Toronto, Univ. of Alberta, Univ. of British Columbia, Queen's Univ., Canadian Wildlife Service, Arctic Institute of North America, and the Dept. of Indian and Northern Affairs. Birds were color banded and removed (LPB only) with permission from the Manitoba Dept. of Natural Resources and the British Columbia Ministry of Environment, Lands and Parks. We thank C. E. Braun and J. F. Bendell for detailed review of the manuscript.

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Wilson Bull., 107(3), 1995, pp. 510–517

NATURAL HISTORY OF THE MONK PARAKEET IN HYDE PARK, CHICAGO

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ABSTRACT.—We studied Monk Parakeets (*Myiopsitta monachus*) in Hyde Park, a residential community in Chicago, Illinois. In April 1992, 64 birds were counted at 26 nests in trees, on utility poles, and on an antenna tower. The population increased to 143 birds in July after nestlings fledged. The following spring, 95 birds were still present at the beginning of the breeding season. Both regionally and locally, the dispersion of nests was clumped. Nesting structures contained one to seven active chambers. The parakeets usually foraged in groups of two to 55 birds on plant buds, weeds, and fruits and berries of ornamental shrubs and tress. During the coldest months of the year, December to February, the birds fed almost exclusively on bird seed at backyard feeders. The generality of the Monk Parakeet's diet, their ability to adapt to a variety of habitats, and their apparent great potential for rapid population growth suggest that they will continue their range expansion and population increase in the United States. *Received 22 Aug. 1994, accepted 1 Feb. 1995.*

The Monk Parakeet (*Myiopsitta monachus*) was introduced into the United States in the late 1960s. A removal program was carried out by the U.S. Fish and Wildlife Service from 1970–1975 (Neidermyer and Hickey 1977), but the species is now widespread in distribution and locally abundant in many localities. On the 1992–1993 Audubon Christmas Bird Counts (CBC), 1343 individuals were recorded in seven states: Connecticut, Delaware, Florida, Illinois, New York, Oregon, and Texas (LeBaron 1993). Monk Parakeets are also known to occur in six other states as well: Alabama, Colorado, Louisiana, New Jersey, Ohio, and Rhode Island (Enser 1992; Summerour 1990; Pruett-Jones, unpubl. records). The Monk Parakeet now appears to be the most abundant and widespread naturalized, non-native parrot species in the United States (see Lever 1987).

Despite their expanding distribution, Monk Parakeets have received little study in the United States. This lack of research is noteworthy considering the status of the species as an agricultural pest in parts of South America (Bump 1971, Bucher et al. 1992). Additionally, the Monk Parakeet is unique among psittacids in that it builds a stick nest, the nests of several pairs may form a large compound nest, and individuals use the nest for roosting throughout the year (Forshaw 1989). The Monk Parakeet is thus a species that should prove extremely interesting, from a behav-

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ioral and ecological standpoint, and one that should be monitored in relation to its potential economic effect on agriculture.

In Chicago, Monk Parakeets were first observed flying free in 1973, and by 1979–1980 they were breeding in Hyde Park. In 1988, the U.S. Department of Agriculture announced plans to destroy this colony, but opposition and a threatened lawsuit by community residents ultimately prevented this. Besides the Hyde Park colony studied here (Fig. 1), the Monk Parakeet is breeding at two other locations in northern Illinois: Bensenville, a suburb west of Chicago where three to five birds have been seen at one nest, and Zion, in the northeastern corner of the state, where two to three birds and one nest have been reported (pers. obs., and pers. comm. from Chicago area bird watchers).

In this study we quantified abundance, nesting dispersion, seasonality of breeding, and diet of Monk Parakeets in the Hyde Park population. Our goal was to establish a population count against which future censuses could be compared and to make observations of natural history of the species in an urban setting. Chicago is not the northern most location where Monk Parakeets occur, but it may be the most severe in terms of winter weather. Understanding the biology of the parakeets in Chicago may help elucidate some of the factors responsible for their population increase in the United States generally.

METHODS

We studied Monk Parakeets from April 1992 to September 1993 in the Hyde Park and Kenwood communities which are approximately 12 km south of Chicago's city center. The study area was approximately 9 km^2 in size and encompassed the entire breeding area of the Hyde Park population of parakeets. It was bounded by 51st Street on the north, 67th Street on the south, Lake Michigan on the east, and Martin Luther King Jr. Drive on the west (Fig. 1). This is a densely populated residential area, but there are open spaces and parkland along the shore of Lake Michigan and in Washington and Jackson Parks (Fig. 1).

Because nesting sites and a given "nest" of Monk Parakeets can involve more than one pair of birds, it is important to clarify terms. We refer to a "nesting area" as a site where one or more nesting structures were located and sufficiently close together that the birds nesting there would normally be in visual contact with each other. The set of birds nesting at each nesting area is equivalent to what Bucher et al. (1992) refer to as a colony. We refer to a "nesting structure" as a stick structure that contained one or more chambers. We refer to an "active chamber" (see Navarro et al. 1992) as a cavity in a nesting structure that birds visited or occupied at any time during a census period.

The nesting structures of Monk Parakeets are both large and conspicuous. We first located all nesting structures on the study area and then censused each site at least every two weeks throughout the study. On each census, we recorded the number of nesting structures, the number of active chambers in each structure, and the maximum number of birds at the nesting area. We spent 30–120 min. at each site during each census and made general observations of the birds' movements, occupancy of cavities, social interactions, nesting building and repair, etc. On a monthly basis, the maximum total number of birds utilizing all sites combined was summed as an estimate of total population size.

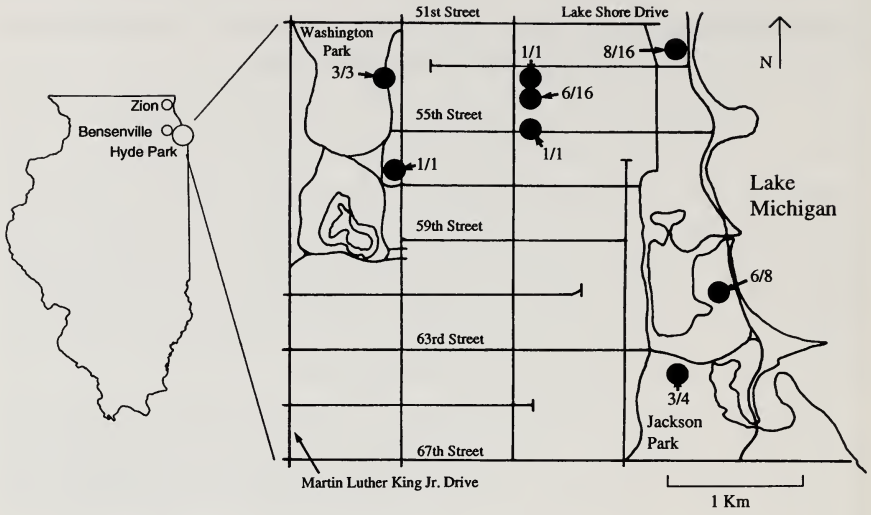

FIG. 1. Distribution of Monk Parakeets in northern Illinois and dispersion of nesting structures in Hyde Park, Chicago, during June 1992. In the Hyde Park map, each darkened circle represents a nesting area. The numbers pointing to each area refer to the number of nesting structures/active chambers in each area. Not all of the residential streets are shown.

We recorded foraging behavior on an opportunistic basis. Every time a foraging bird or group was seen, we noted location, food source, and size of the foraging group. The residential areas and lakefront outside of the study area were occasionally, but not systematically, searched for foraging parakeets.

This study was strictly observational in nature; none of the birds was banded. Although this limited some aspects of the study, we did not assume that we knew the identity of birds when conducting censuses and making other observations. The contents of nests were not physically examined nor were nestlings banded. Fledglings were nevertheless recognizable because juveniles have a whitish area of skin around their eyes; in adults at least one year of age (i.e., all other birds in the population at the start of the study) this area of skin was grayish or generally dark in coloration.

RESULTS

Population census.—A total of 64 birds was counted during April 1992, the first month of census (Fig. 2). Juveniles began to fledge in June, and the population peaked at 143 individuals in July. After July, numbers of individuals declined, presumably because of high mortality of juveniles. By March 1993, the population count was 95 individuals, representing a 46% increase from 1992 to 1993. In September 1993, the last month of census, the population was again large, numbering 171, because of the influx of fledged juveniles.

Distribution of nesting structures.—Thirty nesting structures were found in nine areas in 1992, and 24 nesting structures were located in

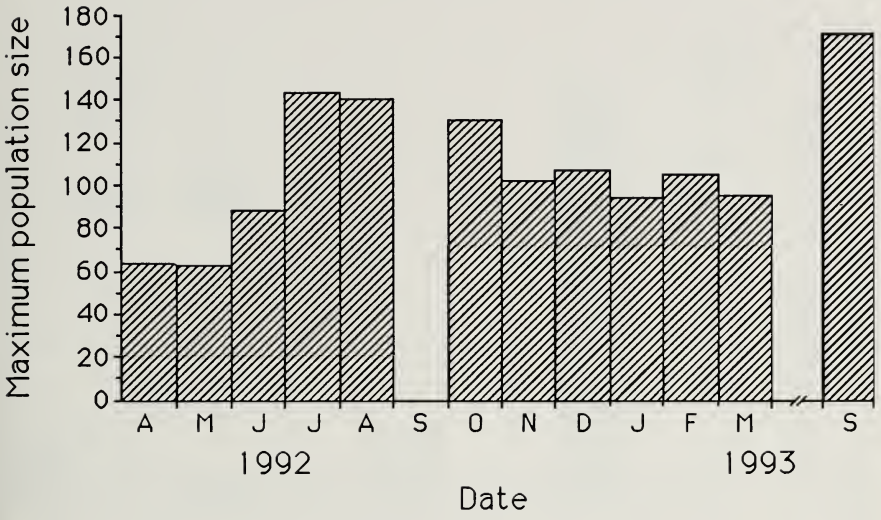

FIG. 2. Monthly population censuses of Monk Parakeets in Hyde Park, Chicago. For each month, the bar graph indicates the maximum number of parakeets observed at all nesting sites combined. No censuses were conducted during September 1992 and from April to August 1993.

seven areas in 1993 (Fig. 1). Each of the seven areas occupied in 1993 had also been used in 1992. Single nesting structures were present at four (44%) nesting areas in 1992 and two (29%) nesting areas in 1993; all other nesting areas had two or more nesting structures. The number of active chambers per nesting structure averaged 1.9 in 1992 (range = 1–7) and 1.6 in 1993 (range = 1–4). In both years, the majority of nesting structures contained just one active chamber (Fig. 3).

Although many nesting structures persisted from one year to the next, a number of them collapsed and were rebuilt. There were also changes in the number of nesting structures at each area. For example, in Washington Park there were four nesting structures in 1992 and six in 1993; at the 53rd street site there were eight nesting structures in 1992 and only three in 1993.

Nesting structures were built in the upper portions of trees (N = 17, 57%), on utility poles (N = 12, 40%), and one nest (3%) was approximately 30 m high on an antenna tower. Of the nine different nesting areas used, six were in parks and three were in residential alley ways.

Seasonality of breeding.—Birds occupied chambers in nesting structures throughout the year. Nevertheless, repair of existing nests and construction of new sites was concentrated in the spring and summer. During 1992, nest building and repair were observed throughout the month of

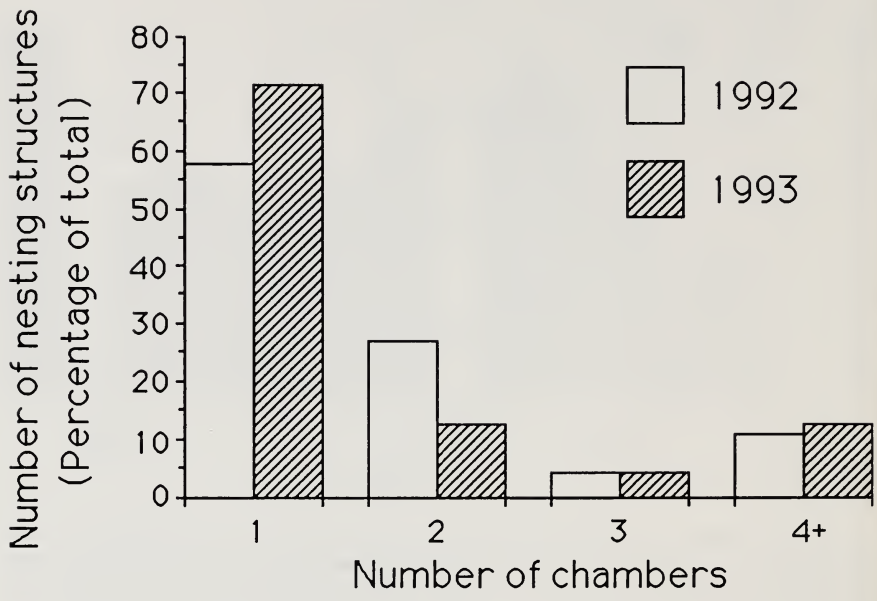

FIG. 3. Frequency distribution of the number of active chambers in nesting structures used by Monk Parakeets in Hyde Park, Chicago during 1992 and 1993.

April and then sporadically until the end of the July. Some juveniles built single-chamber structures in July 1992, but these were not subsequently occupied. In 1993, nest construction and repair began during the first week in March. Repair of minor damage to nests caused by storms was seen at all times of the year.

During 1992, copulations (four total) were observed from 24 April to 25 June. Fledging of young began on 25 June and continued through mid-August. The first two young seen were fully feathered but could not fly and were found on the ground below the nests, appearing to have fallen out of the chambers. Each of these chicks died within a few days. July 2nd was the first date in 1992 when fledglings were seen outside nests and capable of flight. After fledging, juveniles remained in association with their presumed parents and roosted in the nest chamber throughout the autumn and winter months.

Foraging and diet.—The parakeets generally foraged in groups (Fig. 4). Of 167 records of foraging birds, only seven (4.2%) observations were of single individuals. The size of foraging groups averaged 8.7 individuals (range = 1–55). For the three months prior to the fledging of young (April, May, and June), foraging groups averaged 4.7 individuals (N =

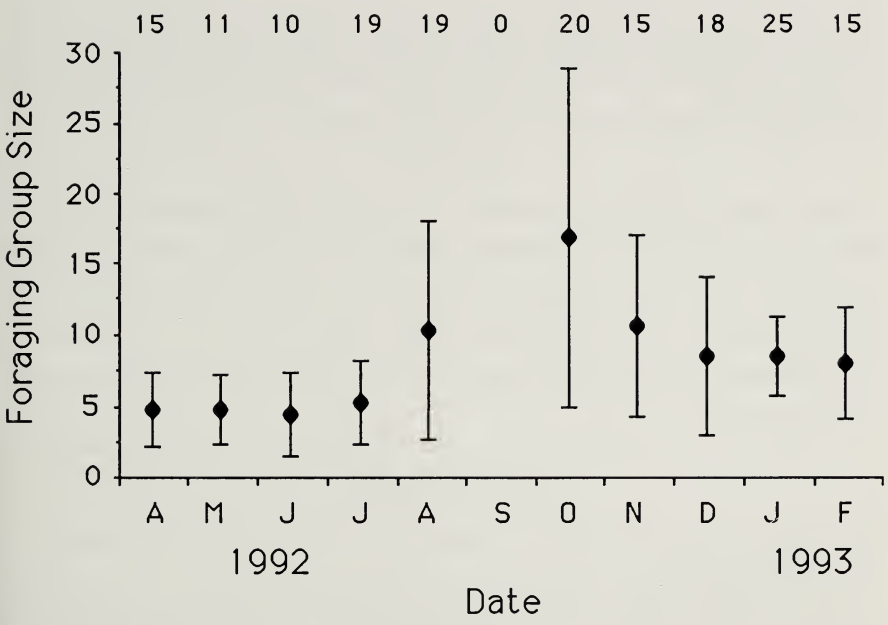

FIG. 4. Monthly change in foraging group size in Monk Parakeets in Hyde Park, Chicago. For each month, the solid circle represents the mean and the vertical bar, the standard deviation, of numbers of parakeets recorded in foraging groups. The sample sizes, the number of groups observed, are indicated across the top of the figure. No observations were made in September 1992.

36, SD = 2.76, mode = 3) in size. From July onwards, foraging groups averaged 9.8 individuals (N = 131, SD = 7.48, mode = 7).

Birds nesting in parks often foraged in other areas of the park away from their nests. We had no evidence that birds travelled great distances out of Hyde Park to forage. On two occasions, however, foraging birds were seen 8 km north of Hyde Park along the lake front, and we suspect that these birds were from our study area.

The parakeet's diet changed during the year. In early spring, the diet consisted of leaf buds from elm tress (*Ulmus* sp.) and weeds such as dandelion (*Taraxacum* sp.) and plantain (*Plantago* sp.). Mulberry trees (*Morus* sp.) then began to produce fruit, and for most of June and July mulberries made up the bulk of the diet. In late summer, the parakeets began to forage on various apple species, from backyard apple trees to ornamental crabapples. The apple supply began to dwindle in early November, and the birds then fed on berries of holly (*Ilex* sp.). As winter approached, holly trees provided the last natural food available, and by mid-December these tree were mostly bare of fruit. From mid-December

to the following March the only abundant food source was bird seed at backyard bird feeders of Hyde Park residents. Except for two observations of birds eating frozen holly berries, bird seed comprised the parakeets' entire diet during these two-and-a-half months.

DISCUSSION

The accuracy of our population estimates depends on the assumption that birds do not visit or occupy chambers at nesting areas other than their own. We had no evidence that birds moved between nesting areas. Birds may have foraged outside the study area, but we are confident that we located all nesting structures within Hyde Park, and we believe that this population represents the only group of nesting parakeets in the greater Chicago area.

It appears that this population of Monk Parakeets is now the largest in the midwestern United States and may be the largest breeding group of parakeets west of the eastern seaboard. The Hyde Park population may be acting as a source population from which birds disperse to other areas in northern Illinois.

On a regional basis, the population of Monk Parakeets in Hyde Park is spatially clumped (Fig. 1). The population is further divided into subgroups which consist of birds occupying each "nesting area" (Fig. 1). The birds from each nesting area foraged together, appeared to exhibit considerable social cohesion, and may comprise the important social unit.

The Monk Parakeets in Hyde Park exhibit many similar aspects of biology and behavior to entirely natural populations within their native range. The findings of Bucher et al. (1992) include, as did ours, that birds nest solitarily or in colonies, individuals occupy nest chambers the year-round, and that young birds continue to roost in nest chambers after fledging.

This study highlights the adaptable nature of the Monk Parakeet in terms of its ability to survive extreme climatic conditions and, when necessary, to adapt itself to a diet of seed provided solely by humans. The population of parakeets in Hyde Park decreased in size during the autumn (Fig. 2), but this may have been due to higher mortality of juveniles. There was no apparent loss of birds throughout the winter months, suggesting that neither the cold temperatures nor a diet of only bird seed increased mortality.

Since the conclusion of the control program by the U.S. Fish and Wildlife Service in 1975, Monk Parakeets in the United States have increased in numbers and expanded their distribution. Elsewhere (Pruett-Jones and Hyman, unpubl. data) we estimate that there are 3000 to 5000 Monk Parakeets in the United States but consider this estimate conservative.

The species is likely to continue its population increase, since Monk Parakeets are adaptable to urban and suburban habitats. They have, at least in Chicago, become endeared to city residents who are willing to go to great lengths to protect them. They also have characteristics that can facilitate rapid population growth, including a nearly omnivorous diet (see Lever 1987) and a large reproductive output (Navarro et al. 1992).

Whether the Monk Parakeet poses a threat to agriculture in the United States remains to be seen (see Neidermyer and Hickey 1977). It certainly has the potential to do so if large populations occur near grain fields or fruit orchards as has happened in South America (Bucher et al. 1992). A separate problem caused by Monk Parakeets in the United States is damage to electrical substations because of their large nesting structures. In Houston, Texas, nests are first trimmed and ultimately removed if they present a hazard (B. Baker, pers. comm.).

ACKNOWLEDGMENTS

We thank the Univ. of Chicago Undergraduate Research Program (JH), the Dept. of Ecology and Evolution, University of Chicago, and the National Science Foundation (SP-J) for support, and the numerous individuals that shared their observations of Monk Parakeets with us. M. Pruett-Jones and M. Webster offered helpful suggestions on earlier versions of the manuscript.

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Wilson Bull., 107(3), 1995, pp. 518–529

SUCCESSFUL NESTING BEHAVIOR OF PUERTO RICAN PARROTS

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ABSTRACT.—We analyzed nesting behavior of five pairs of the endangered Puerto Rican Parrot (*Amazona vittata*) during eight successful nesting attempts. Each stage of the nesting cycle (egg laying, incubation, early chick rearing, and late chick rearing) was characterized by distinct trends or levels of behavior. During egg laying, female attentiveness to the nest increased, and male attentiveness decreased. Throughout incubation and the first several days of early chick rearing, females were highly attentive to their nests, whereas males rarely entered the nest cavities. Female attentiveness then began to decline. Male attentiveness to the nest was sporadic until chicks were 10–12 days old, when all males began to enter their nests at least once each day. During late chick rearing, both male and female attentiveness were erratic and highly variable. Biologists may be able to use these results to identify nest problems and the need for management intervention when patterns of nest attentiveness deviate from the limits described in this study. *Received 26 Apr. 1994, accepted 15 Jan. 1995.*

Manipulation of reproductive behavior is often an important component of recovery programs for endangered birds. Behavioral manipulations have been used to increase productivity by inducing individuals to lay additional eggs through the removal of clutches (Cade 1977, Fyfe et al. 1977, Snyder and Hamber 1985), by artificially incubating eggs to increase hatchability (Cade 1977), and by hand-rearing or fostering into nests those chicks that otherwise would not have survived (Cade 1977, Meyburg 1977). "Hacking" and cross-fostering have been used to increase fledging rates in the wild (Fyfe et al. 1977, Meyburg 1977), to establish new populations (Drewien and Bizeau 1977, Kress 1977) and to establish new nest site or habitat preferences within a species (Cade 1977, Drewien and Bizeau 1977, Temple 1977).

The Puerto Rican Parrot (*Amazona vittata*) is critically endangered, with only 42 individuals remaining in the wild (1994 post-breeding survey, J. Meyers, pers. comm.). Monitoring and manipulation of reproductive behavior have been an important part of the U.S. Fish and Wildlife Service's Puerto Rican Parrot Recovery Program since 1973 (Snyder et al. 1987). Biologists have increased parrot productivity by inducing re-

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placement clutches, by fostering captive-produced young into wild nests, and by intervening when eggs or chicks are in jeopardy (Wiley 1981, 1985; Snyder et al. 1987; Lindsey 1992).

Because Puerto Rican Parrots nest in cavities and are sensitive to disturbance (Snyder et al. 1987, Wilson 1993), biologists responsible for monitoring parrots' nesting activities usually rely on behavioral cues from breeding pairs to determine if intervention is needed. Currently, evaluation of pair behavior depends largely on observers' personal experiences because few specific guidelines for identifying indicators of potential nest problems are available. Parrot managers, biologists, and nest observers (particularly new or seasonal personnel) need additional guidelines to maximize the effectiveness of nest monitoring and management.

The purpose of this study was to provide a detailed description of adult Puerto Rican Parrot nest attentiveness during successful nesting attempts.

STUDY AREA AND METHODS

During the study period, Puerto Rican Parrots nested in four distinct valleys within the Caribbean National Forest, an 11,300-ha section of the Luquillo Mountains in northeastern Puerto Rico (18°19′N, 65°45′W). All four valleys were within the Colorado Forest vegetation association described by Wadsworth (1951) and were dominated by palo colorado (*Cyrilla racemiflora*). Snyder et al. (1987) reported that three of the four areas included in our study were 510–625 m above sea level, received mean annual rainfall of 342.4–399.0 cm, and had an approximate temperature range of 16–29°C during 1974–1978. Although no data from the fourth valley in our study area were collected, we believe it possessed characteristics similar to those described above.

We (KAW and MHW) collected data and supervised data collection by 31 staff and volunteers in the nest guard program conducted by the U.S. Fish and Wildlife Service (Lindsey 1992). From February to August, 1987–1990, nests were monitored approximately 80–94% of all days in which a nest contained eggs or chicks (Lindsey 1992). Observers monitored nesting activity from blinds 10–30 m from each nest and recorded activities of breeding pairs. Individual parrots were identified primarily by size and pattern of the red blaze on each individual's forehead and secondarily by body shape and coloration. In 1989 and 1990, a microphone attached to a remote listening device was installed in each active nest; observers then monitored sounds in the nest cavity to confirm parrot movements.

In this paper, we examined only data from successful nesting attempts. We defined successful nesting attempts as those that involved no manipulation of eggs and that fledged at least one chick without the assistance of management intervention. We will examine adult behavior during failed nesting attempts in a separate publication.

We calculated the date that the first egg of each clutch was laid (day 0), based on inspections of each nest. If eggs were found during the first inspection, we assumed that one egg was laid every other day (Rodriguez-Vidal 1959, Low 1986, Snyder et al. 1987) and that no eggs were laid on the day of the inspection unless consecutive inspections indicated otherwise. If no inspection was performed during early stages of a nesting attempt, we backdated from estimated hatch dates, based on a 26-day incubation period (Snyder et al. 1987). Because Puerto Rican Parrots begin incubation between laying their first and second eggs in a 2- to 4-egg clutch (Snyder et al. 1987) and because nest inspections were infrequent during egg laying, the estimated error for calculation of egg laying date was ± 2 days. One

nest that was relatively inaccessible had an estimated error for calculation of egg laying date of ± 5 days.

We divided the nesting cycle into four stages: egg laying (day −2 through day 6), incubation (day 7 through day 26), early chick rearing (day 27 through day 47), and late chick rearing (day 48 through fledging). We calculated mean, range, and standard error of the mean for five behavioral components for each day of the nesting cycle. Each data point (which represented the behavior of the male or female during one nesting attempt) included in these calculations was based on 15 h of observation per day (05:00–20:00, EST). Actual observation periods began at dawn (05:30–06:30) and ended at dark (18:00–19:30). We assumed that variations in actual daylight hours did not bias our results. Because breeding female Puerto Rican Parrots tend to roost in the nest cavity throughout the nesting cycle and because their mates tend to roost in the canopy near the nest tree (Snyder et al. 1987), we assumed that parrots did not enter or leave the nest in darkness. Data from days on which observers missed the parrots' movements (because of darkness or for other reasons) were not included in our calculations. Because of excluded data and because not all nests were observed on all days, the number of nesting attempts in our analysis (N) varied from day to day.

We examined five behavioral components. The first component, nest attendance, was measured as the percentage of a 15-h period that a parrot spent in its nest cavity. Our calculation of nest attendance included only periods when the parrots were in the cavity, not when they were perched on the nest lip or outside the cavity. Frequency of nest entries was the number of times a parrot entered its nest during a 15-h observation period. Mean attentive period was defined as the average time a parrot spent in its nest during each nest visit. Overnight attentive periods were not included in our calculations of mean attentive periods. Mean recess was the average time a parrot spent outside the nest each time it left the cavity. We calculated this component only for females. The fifth component, longest recess, was defined as the longest time a parrot spent away from its nest at any one time. We calculated this component only for females. Although these five behavioral components were interrelated, we described each component for the four stages of the nesting cycle to provide a more complete description of each parrot's behavior.

Nesting attempts by the same pair were not truly independent, but we treated each nesting attempt as a separate event because each new clutch offered the pair an opportunity to succeed or to fail in raising their young. Descriptive statistics were used to present the results of this study. More rigorous statistical tests were not applied to these data for two reasons. First, small sample size can lead to high probability of Type II error (Siegel 1956). Second, these data are not samples of a larger population but, to the best of our knowledge, the entire population of wild Puerto Rican Parrots that successfully reproduced during the study period.

Snyder et al. (1987) reported a similar data set that described behavior of Puerto Rican Parrots nesting in the Luquillo study area during 1973–1978. However, methods used by Snyder et al. (1987) to analyze raw data were sufficiently different from those used in our study that a direct comparison of these two data sets would have been inappropriate.

RESULTS

Eight of 15 nesting attempts observed during our data collection were classified as successful; one pair made three successful nesting attempts, one pair made two successful nesting attempts, and three pairs made one successful nesting attempt each. Six nesting attempts resulted in two fledged chicks each, and two attempts resulted in three fledged chicks

each. Although no serious threats to reproductive success occurred during these nesting attempts, these nests did receive management attention. For example, all chicks were weighed periodically, and, in some cases, chicks were added, exchanged, or removed from nests (e.g., to increase genetic variability of the captive flock). However, in our judgment, these activities did not alter the likelihood of successful fledging of the remaining young.

Female parrots increased their nest attendance (Fig. 1), spent more time in their nests during each visit (Fig. 1), and took shorter recesses as egg laying progressed (Fig. 2). Three females exhibited no distinct trend in frequency of nest entries during egg laying, whereas one female, who entered her nest frequently during early egg laying, decreased her number of entries as she settled into incubation. Most males rarely entered their nests during egg laying (Fig. 3). One male, however, entered his nest frequently during early egg laying during two of his three nesting attempts. During these two nesting attempts, this male entered his nest less frequently and spent less total time on his nest as egg laying progressed.

During incubation, females maintained high levels of nest attendance (Fig. 1) and spent only brief periods away from their nests (Fig. 2). We found little variability in female nest attendance (Fig. 1), mean recesses (Fig. 2), or longest recesses (Fig. 2) within or among nesting attempts. No trend in frequency of nest entries was apparent (Fig. 1). After an incident of human disturbance (day 23), however, one female entered her nest more frequently and spent less time in her nest during each visit than did other females during this stage (Fig. 1). Males entered their nests infrequently during incubation and spent only brief periods in their nests when they did enter (Fig. 3).

During early chick rearing, females became less attentive to their nests (Fig. 1), whereas male attentiveness increased (Fig. 3). Females maintained high nest attendance during the first four days of early chick rearing (Fig. 1); thereafter, attendance declined, mean attentive periods became shorter (Fig. 1), and periods away from the nest increased (Fig. 2). Variability in female nest attendance (Fig. 1) and in duration of periods off the nest (Fig. 2) within and among nesting attempts also increased. Females tended to enter their nests more frequently during the first half of early chick rearing; their frequency of nest entries then stabilized (Fig. 1). High day-to-day variability within nesting attempts, however, obscured any trends in behavior of individual parrots. One female spent an unusually long time off her nest on day 41 following incidents of human disturbance on consecutive days; her mean recess increased, and her longest recess was more than twice as long as those of other females during this stage (Fig. 2). Males entered their nests sporadically during the first half of early chick rearing, but their nest attendance and frequency of entries

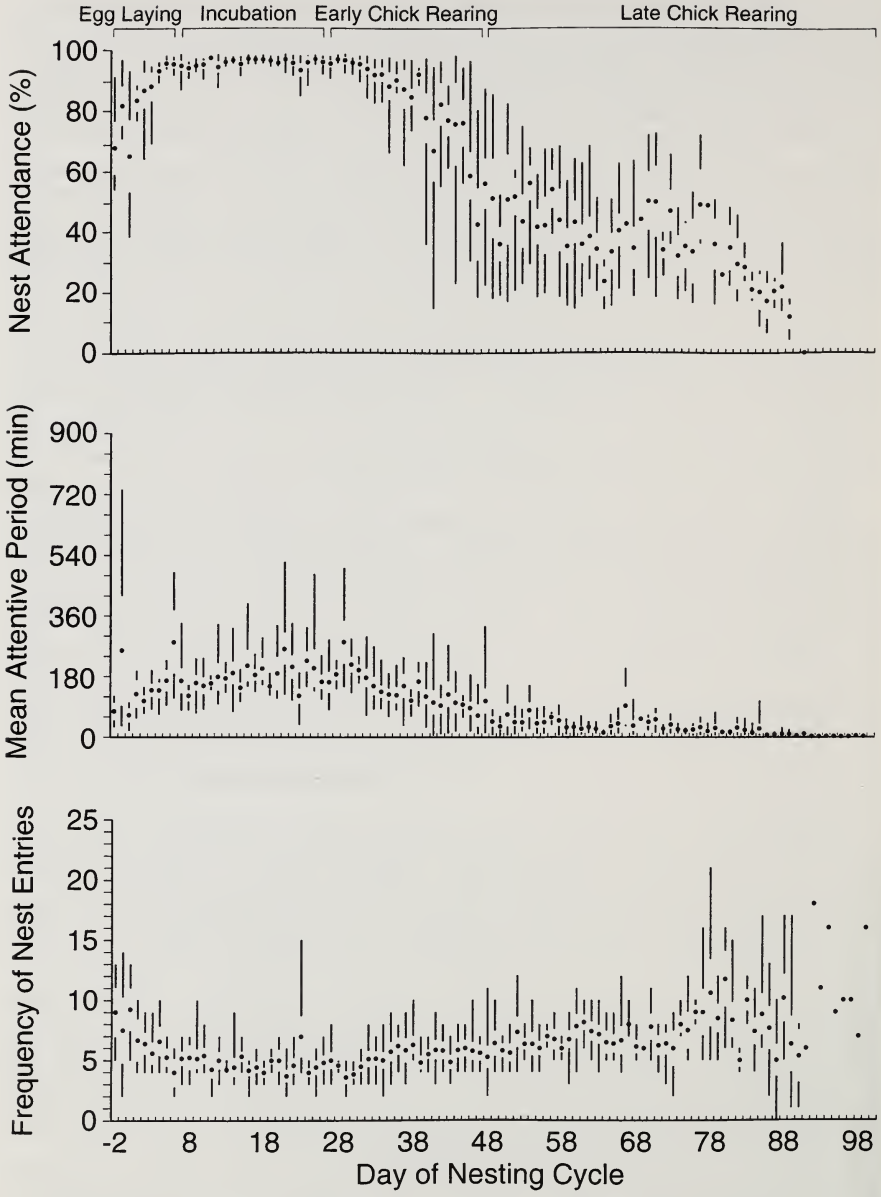

FIG. 1. Nest attendance (percentage of a 15-h period spent in the nest cavity), mean attentive periods (average period in nest during each visit), and frequency of nest entries (number of visits per day) by female Puerto Rican Parrots that experienced successful nesting attempts during four nesting stages, 1987–1990. Mean (black dots), standard error (gap in black bars), and range (black bars) are shown for all observed nests for each day of the nesting cycle. Sample size (N) varied daily from one to eight nesting attempts.

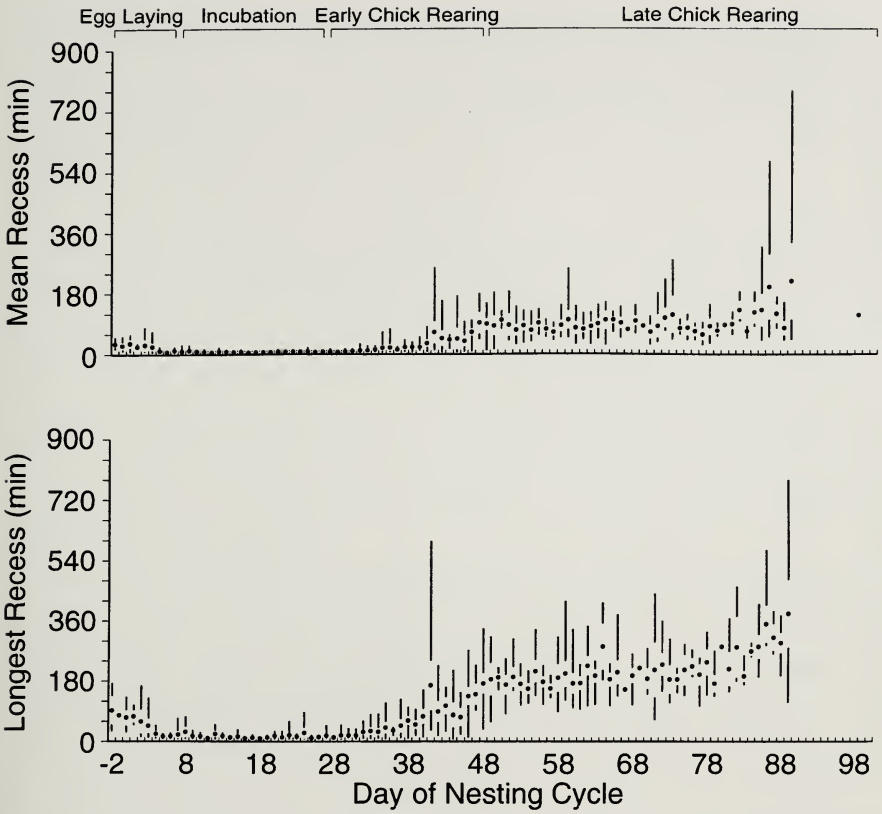

FIG. 2. Mean recesses (average period out of nest) and longest recesses (longest period out of nest) by female parrots that experienced successful nesting attempts during four nesting stages, 1987–1990. Other aspects of this figure are the same as those noted in Fig. 1.

generally increased as chick rearing progressed (Fig. 3). Except for one incident (one male on day 48), all males entered their nests at least once each day after their chicks were 10–12 days old (approximately day 38 of the nesting cycle) (Fig. 3).

During late chick rearing, female nest attendance varied erratically within and among nesting attempts (Fig. 1). At the end of the nesting cycle, however, females decreased their attendance (Fig. 1), spent less time in their nests during each visit (Fig. 1), and took longer recesses (Fig. 2). Variability in frequency of nest entries increased during the last several days of the nestling period as females entered their nests more frequently or fed their chicks from the nest lip as the chicks came to the top of the cavities (Fig. 1). Males entered their nests regularly and spent

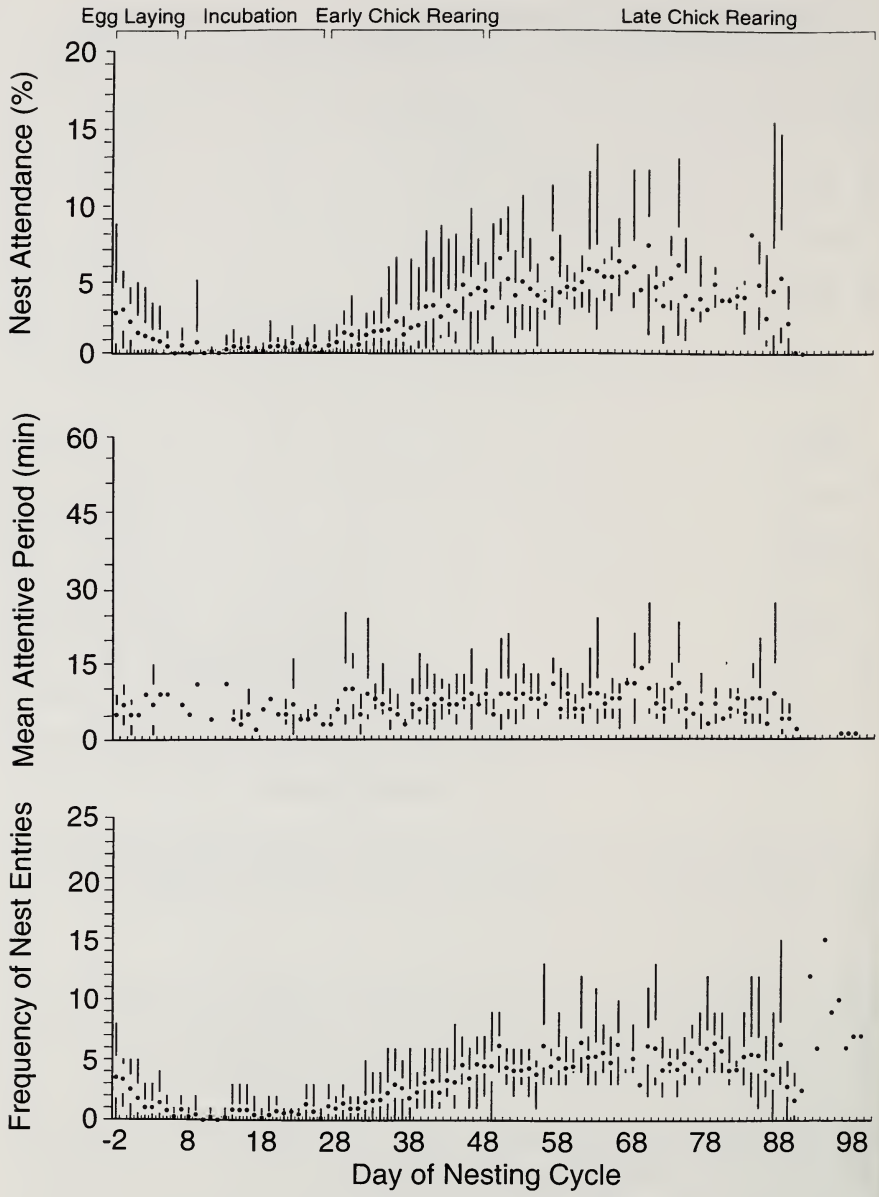

FIG. 3. Nest attendance (percentage of a 15-h period spent in the nest cavity), mean attentive period (average period in nest during each visit), and frequency of nest entries (number of visits per day) by male parrots that experienced successful nesting attempts during four nesting stages, 1987–1990. Note that the scale is different from that used in Fig. 1. Other aspects of this figure are the same as those noted in Fig. 1.

only brief periods of time in their nests throughout the late chick-rearing period; their behavior showed no distinct trends (Fig. 3). Like females, some males entered their nests more frequently and spent more time in their nests just prior to fledging of their young, whereas others fed their young from the nest lip (Fig. 3).

DISCUSSION

Puerto Rican Parrots that successfully raised their young exhibited distinct patterns of nesting behavior during incubation and early chick rearing. During incubation, females maintained high nest attendance and took only brief recesses from the nest, whereas males rarely entered nest cavities. Females spent less time in the nest as chick rearing progressed, whereas males entered their nests more frequently and increased their nest attendance. These distinct patterns of behavior reflect the importance of the incubation and early chick-rearing periods to successful reproduction, as eggs and young chicks are vulnerable to predation, temperature variation, and nutritional stress.

Although we observed little harassment of Puerto Rican Parrots by predators during our study, patterns of nest attentiveness exhibited by this species may be an adaptive response to predation pressure. Red-tailed Hawks (*Buteo jamaicensis*) have been reported to prey upon nestlings (Snyder et al. 1987) and fledglings (Lindsey et al. 1991) and have been observed harassing adults (Snyder et al. 1987). Unattended eggs and young chicks are vulnerable to predation or injury by Pearly-eyed Thrashers (*Margarops fuscatus*), introduced rats (*Rattus* spp.), and Puerto Rican boas (*Epicrates inornatus*) (Snyder et al. 1987). Infrequent nest entries may reduce the probability of revealing nest location to predators, whereas long attentive periods and high overall nest attendance allow almost constant defense of nest contents (Skutch 1957, 1962). Other behaviors of the Puerto Rican Parrot, such as the secretive movements of adults in the nest area and a tendency to allofeed close to the nest during incubation, also may reduce the conspicuousness of the nest and adults (Snyder et al. 1987).

Behavior of female parrots during early chick rearing reflects the changing thermoregulatory and nutritional needs of their young. Females maintain high nest attendance while chicks are dependent on almost constant brooding for survival; extended absences at this time can cause death of the young from exposure. Low (1986, 1987) noted that even if young do not succumb outright, chilling can leave them too weak to beg, increase their susceptibility to disease, and cause poor digestion and decreased growth rates. As the young develop thermoregulatory abilities, females spend more time away from their nests. Although Gnam (1991)

found that size of Bahama Parrot (*Amazona leucocephala bahamensis*) broods did not affect the amount of time that females spent off the nest, Snyder et al. (1987) noted that female Puerto Rican Parrots with larger broods reached a plateau of time off the nest sooner than did females with smaller broods. Members of a brood tend to huddle together and, therefore, reduce the probability of chilling; however, larger broods also require more food. Females with larger broods may need to forage earlier in the nesting cycle for young to achieve optimal growth rates. There was too little variability in brood size in our study to make similar observations.

Behavior of males during early chick rearing appears to be related to nutritional needs of the young. Males almost invariably visited their nests daily (and presumably fed their young) after the chicks were approximately 10 days old; regular allofeeding by males may be essential for proper growth of the young at this time. During a nesting attempt reported by Snyder et al. (1987), chicks had notably slower rates of growth immediately following the loss of the adult male; although growth rates increased and the chicks later fledged, they remained underweight through the last recorded measurements at 34 and 37 days of age.

During late chick rearing, behavior within and among nesting attempts was highly variable. Nest attendance by females varied erratically, both within and among nesting attempts, and males showed no distinct patterns of behavior. We were unable to examine many potential causes of variability in this study because of small sample size and insufficient data; however, other authors have noted that variability in patterns of reproductive behavior of psittacines has been associated with previous reproductive experience (Noegel 1979; Thompson 1983; Low 1986, 1987; Stoodley and Stoodley 1990; Silva 1991), food supplies (Saunders 1977), weather (Saunders 1977, Gnam 1991), disturbance (Snyder et al. 1987, Wilson 1993), and individual differences (Low 1986, Stoodley and Stoodley 1990).

Aviculturists have noted that inexperienced *Amazona* often fail to provide adequate care for their young. For example, Low (1986, 1987) and Thompson (1983) noted that inadequate feeding of young by inexperienced *Amazona* is not uncommon. Although all pairs in our analysis fledged at least two chicks (which required adequate feeding and care of at least a partial brood), differences in previous experience among pairs may have accounted for some of the variability in behavior of adults among nesting attempts (e.g., frequency or duration of nest visits).

Saunders (1977) reported that White-tailed Black Cockatoos (*Calyptorhynchus baudinii latirostris*) that nested where food was patchily distributed spent less time in their nests and fed their chicks less frequently

than did adults that nested in areas with more abundant food. Many of the most important food plants (particularly sierra palm, *Prestoea montana*) used by Puerto Rican Parrots are patchily distributed (Snyder et al. 1987); variability in behavior may reflect, in part, differences in the distances that pairs move in order to find food.

Female Bahama Parrots usually cease roosting in the nest by the fourth week post-hatching (Gnam 1991). However, Gnam (1991) noted that a female Bahama Parrot that had ceased roosting in the nest at night returned to brood during a period of heavy rainfall. In addition, Saunders (1977) noted that White-tailed Black Cockatoos spent less time foraging as temperature increased and therefore tended to feed their young less frequently on hot days. Although we did not measure precipitation or ambient temperature during our study, we know that three of the four valleys included in our study area received mean annual rainfall of 342.4–399.0 cm during 1974–1978 and are 510–625 m above sea level (Snyder et al. 1987). Differences in the location of each nest, as well as daily or annual variation in rainfall or the temperature fluctuations that often accompany rainfall, may have contributed to variability in nesting activities.

Disturbance from territorial intrusions by other parrots may cause defensive behavior by breeding pairs (Snyder et al. 1987). In extreme cases, excessive competition for nest sites has resulted in abandonment of active nests or injury to Puerto Rican Parrots (Snyder et al. 1987). In addition, human activities in nest areas affected the behavior of nesting females. During this study, females sometimes entered their nests more frequently and took longer recesses following incidents of human disturbance; Wilson (1993) provides a more detailed account of the effects of disturbance on the behavior of nesting adults.

Stoodley and Stoodley (1990) noted individual differences among female *Amazona* in frequency of allofeeding and in their ability to care for their young. Low (1986) noted that the age of the young when first fed by their male parent and the frequency of subsequent feedings varied among individual males. The relative contributions of inheritance and learning to such variation are unknown.

Although our sample size is small, our results indicated that a successful nesting attempt by Puerto Rican Parrots was characterized by well-defined patterns of attentiveness to the nest during incubation and early chick rearing. During incubation and the first several days of early chick rearing, females spent little time outside the nest and males rarely entered nest cavities. As chick rearing progressed, female nest attendance declined and males established a regular pattern of nest entries. Because these measures of attentiveness represented well-defined patterns of behavior, they may be particularly useful to parrot managers. If one assumes that

variability of these measures defines the limits of normal behavior for each stage of the nesting cycle, deviations from the patterns described in this study may indicate nest problems that require management intervention.

ACKNOWLEDGMENTS

We thank the many volunteers in the Puerto Rican Parrot Nest Guard Program and the staff of Puerto Rico Research Group for collecting data used in this study. The Student Conservation Association, National Audubon Society, National Fish and Wildlife Foundation, and U.S.D.A. Forest Service, Caribbean National Forest and Institute of Tropical Forestry provided financial and logistical support for the volunteer program. Constructive review comments on drafts of this manuscript were made by Noel F. R. Snyder, James W. Wiley, Dirk V. Lanning, Gerald D. Lindsey, and Thane K. Pratt. This study was funded by the Endangered Species Research Branch, Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service (now National Biological Service), Laurel, Maryland, through a Research Work Order to the Massachusetts Cooperative Fish and Wildlife Research Unit. Cooperators of the Massachusetts Unit are the National Biological Service, University of Massachusetts, Massachusetts Division of Fisheries and Wildlife, Massachusetts Division of Marine Fisheries, and Wildlife Management Institute.

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Wilson Bull., 107(3), 1995, pp. 530–537

LIFE HISTORY AND ECOLOGY OF FLAMMULATED OWLS IN A MARGINAL NEW MEXICO POPULATION

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Abstract.—In 1981–1986, we studied Flammulated Owls (*Otus flammeolus*) nesting in a forest-woodland ecotone at the species' lower elevational limit. Most adults did not renest in the same tree cavity despite previous success. Clutch size was smaller, and eggs were less likely to produce fledglings than in a coniferous forest population studied concurrently by Reynolds and Linkhart (1987b). Additional features of life history and nesting density were similar to other populations, but nesting mass of females and productivity were lower, while density flux was higher. Our study population is marginal ecologically, perhaps limited by food shortage during courtship plus predation and maintained by immigration. *Received 25 April 1994, accepted 15 Feb. 1995.*

The Flammulated Owl (*Otus flammeolus*) nests in tree cavities in mature coniferous forest, largely in ponderosa pine (*Pinus ponderosa*) and mixed conifer associations (McCallum 1994a, b). Its small mass, clutch of two or three eggs, and migratory habits differ from congeners such as the Eastern Screech-Owl (*Otus asio*), a larger permanent resident with a larger clutch (Gehlbach 1994). Here we analyze the life history and ecology of Flammulated Owls in a marginal ecological situation in New Mexico and compare them with other populations and the Eastern Screech-Owl.

STUDY SITE AND METHODS

Cottonwood Gulch (CWG), our study site 12 km South of Thoreau, McKinley County, New Mexico, was described by McCallum and Gehlbach (1988). The vegetation is mature and ecotonal between ponderosa pine forest and pinyon (*Pinus edulus*)-juniper (*Juniperus* spp.) woodland at 2230–2277 m in the Zuni Mountains. This is the lower elevational limit of Flammulated Owls locally (they nest to at least 2780 m). Because we make detailed comparisons with Flammulated Owls in central Colorado, it is important to note that this population lives at 2550–2855 m in coniferous forest more typical of the species and was studied concurrently by Reynolds and Linkhart (1987a, b).

At CWG, call surveys and searches of all possible tree cavities were made annually during late April-early July, 1981–1986, in a 160 ha plot. Small owl population highs and lows are 3–4 years apart on average (Korpimaki 1981, Gehlbach 1994), so we tried to study the population during at least two cycles. Before recording any nesting data for analysis, we allotted at least a week of owl-human habituation time. At two nests with nestlings and

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fledglings in 1982, foraging by both adults was recorded in the first hour after sunset (11 h total). In 1983, we made all-night observations of feeding rates at four nests in incubation and nestling periods (141 h total). Other field techniques are elaborated in Gehlbach (1994), the source of comparative information on other owls, particularly the Eastern Screech-Owl.

We mapped suitable cavities (McCallum and Gehlbach 1988) and nest sites on a 1:8700 aerial photo. Locations, physical features, and habitat boundaries were digitized using ERDAS program Digpol and a GTCO Digi-pad. Data analyses included parametric and nonparametric statistics and transformations appropriate to two-sided tests (SAS Inst. 1988, Wilkinson 1990a). We used the $P = 0.05$ alpha level of significance. Summary statistics are mean ± one standard deviation unless otherwise stated.

RESULTS

Habitat and nest sites.—Flammulated Owls selected 14 nest cavities 260 ± 147 m from nearest-neighbor nest sites in mature (open) vegetation typical of the species (McCallum and Gehlbach 1988, McCallum 1994a, b). Nest sites tended toward regular spacing (R = 1.4, Clark and Evans 1954), and most (79%) were within 50 m of grassland. Other than two sites that faced grassy openings at the edges of ponderosa pine thickets, dense saplings were avoided except for roosting.

We found 39 nest cavities and useable alternatives, 7.8 times the number needed to house the maximum density of five breeding pairs. The cavity surplus and lack of inter- or intra-specific disputes over cavities suggests that our birds were not site limited (also the case in Eastern Screech-Owls). For example, Flammulated Owls and Mountain Chickadees (*Parus gambeli*) nested simultaneously in the same pine twice without conflict, once in cavities on opposite sides of the tree at nearly the same height.

Three Flammulated Owl nests housed nesting colonies of *Liometopum occidentale,* an ant that attacked us, producing painful bites and stings when we investigated owl eggs and nestlings. The owls were not bothered and fledged all chicks successfully. A similar potentially protective relationship between tree ants and Eastern Screech-Owls has been described and observed once in Western Screech-Owls (*O. kennicottii*). This may be a unique symbiosis in *Otus,* although it seems to be infrequent.

Site fidelity.—None of 13 banded nestlings was recaptured at CWG, nor were nestlings recaptured in Colorado (Reynolds and Linkhart 1987a, 1990). Among 18 nesting adults, only a male and four females (28%) returned to our study plot in subsequent years. By contrast, the return rate was 55% for 20 adults in Colorado, but this is not a significant difference, perhaps because of the small samples (Fisher's Exact $P = 0.27$).

Of the five returnees at CWG, only one female used the same nest cavity more than once (repeated twice). Failure to reuse a cavity followed three nest failures but also 14 successes at CWG, similar to the species

in Oregon (Goggans 1986) and British Columbia (Van Woudenberg 1992), unlike the Eastern Screech-Owl which reuses cavities after successes not failures.

Four breeding dispersals averaged 423 ± 126 m, no different than five in Colorado (mean 474 m; $t = 0.8$, ns). The mean is about one territory diameter, based on an average diameter of 424 m in Colorado (Reynolds and Linkhart 1987a) and is 1.6 times the mean distance between neighboring nest cavities, suggesting that our owls moved only about one territory away before nesting again as their counterparts did in Colorado.

Breeding density.—Nests per 100 ha averaged 2.9 ± 1.5 (5 yr), a value slightly higher than nests in Colorado (2.1 ± 0.8, 4 yr; Reynolds and Linkhart 1987b) and Oregon (1.4 ± 0.3, 2 yr; Goggans 1986). Mean differences are not significant, however ($F = 1.5$, ns). Density flux, measured by the coefficient of variation, was 0.52 at CWG compared to only 0.38 in Colorado and 0.21 in Oregon.

Because four nest sites were near edges of our study plot, which was smaller than plots in Colorado and Oregon, we calculated minimal spanning distances of trees at all nest sites and used the annual mean distances as area-independent estimates of density (Wilkinson 1990b). These distances were 519 m at CWG (5 yr) and 472 m in Colorado (2 yr, calculated from Linkhart 1984), substantiating the similarity of population densities based on nest counts (Mann-Whitney $U = 7$, ns).

Productivity.—Mean clutch size was 2.3 ± 0.5 (N = 11) and brood size 2.2 ± 0.6 (N = 10). Hatchability (mean brood/mean clutch) was 0.96. Fledglings in 10 nests were 1.8 ± 0.8, hence fledgability (mean fledglings/mean nestlings) was 0.82. Ten of 12 nests fledged chicks, a success rate of 0.83, multiplied by the product of hatchability and fledgability (0.79) to give an estimated productivity of 0.65 fledglings per egg or 1.5 per nest. This is significantly lower ($t = 2.4$, $P = 0.04$) than 0.74 fledglings per egg and the mean of 2.3 per nest in Colorado (Reynolds and Linkhart 1987b, McCallum 1994b), partly because clutches at CWG are smaller (mean 2.7 in Colorado; $t = 2.3$, $P = 0.03$).

Egg and adult mass.—Mean egg mass was 10.4 ± 0.4 g (N = 9). Eight incubating females weighed 69.9 ± 8.4 g, dropping to 63.1 ± 1.2 g at hatching of the last egg (estimated from regression), and six with nestlings weighed 59.7 ± 5.8 g. The loss was estimated as 0.52 g/day by regressing the masses of seven females, each weighed at least three times, on nestling age with Julian date and female identity as covariates. Controlling for among-individuals variation, nestling age explained a significant 42% of the variance in female mass ($r^2 = 0.90$, $P < 0.001$).

By contrast, incubating and brooding females in Colorado were significantly heavier with means of 78.3 g (incubation) and 63.3 g (nestlings,

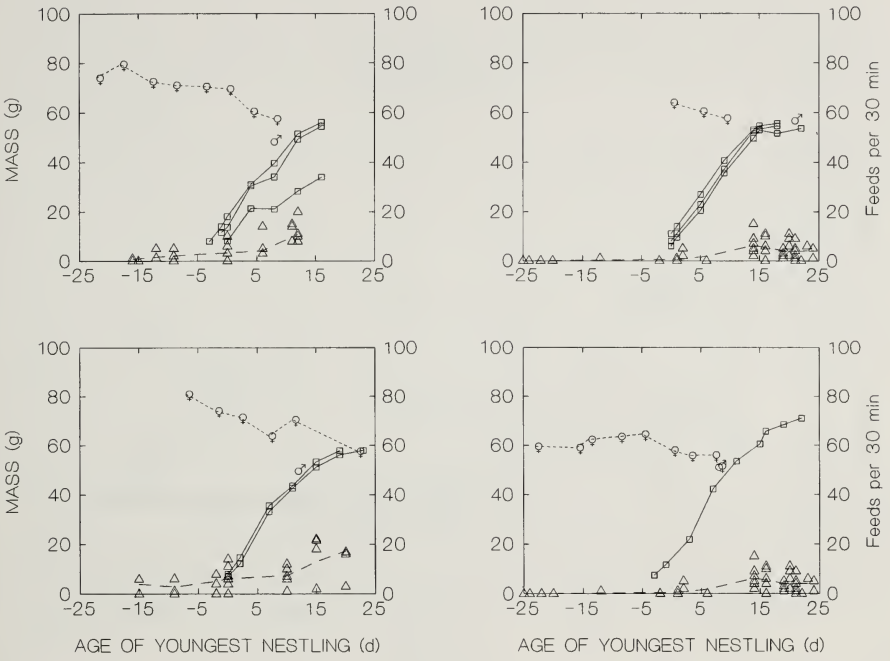

FIG. 1. Mass of adult females (short dashes), males (single symbols), and their nestlings (solid lines) in relation to age of youngest nestling in each of four nests, 1983. Feeding visits between sunset and midnight are triangles (long dashes); trends fitted by robustly weighted regressions.

$t > 1.9$, $P < 0.03$; data from Reynolds and Linkhart 1987b). However, eight males delivering food to nestlings at CWG weighed 52.5 ± 3.3 g, essentially like their counterparts in Colorado (mean 53.2 g).

Chick growth, fledging, and provisioning.—Seven hatchlings weighed 6-8 (7.5 ± 0.8) g and grew to 48-71 (56.2 ± 5.9) g at fledging, similar to Colorado owlets. Growth was sigmoid but did not level off at fledging (Fig. 1), as in Colorado, suggesting that chicks vacate their nest cavity a few days before they can fly as do the chicks of Eastern Screech-Owls. Three fledged at 23.7 ± 2.1 d of age, fluttered to the ground, and walked, hopped, and climbed trees with bills, feet, and flapping wings like fledgling Eastern Screech Owls. Their nestling period was the same as in Colorado (mean 23.0 d, $t = 0.5$, ns; data from Reynolds and Linkhart 1987b). The upper left graph in Fig. 1 shows the reduced growth rate of a last-hatched chick found dead in the nest after its siblings fledged, while the lower right graph shows the unusually large mass of a single nestling that fledged at 26 d. These contrasting examples, and two other cases of

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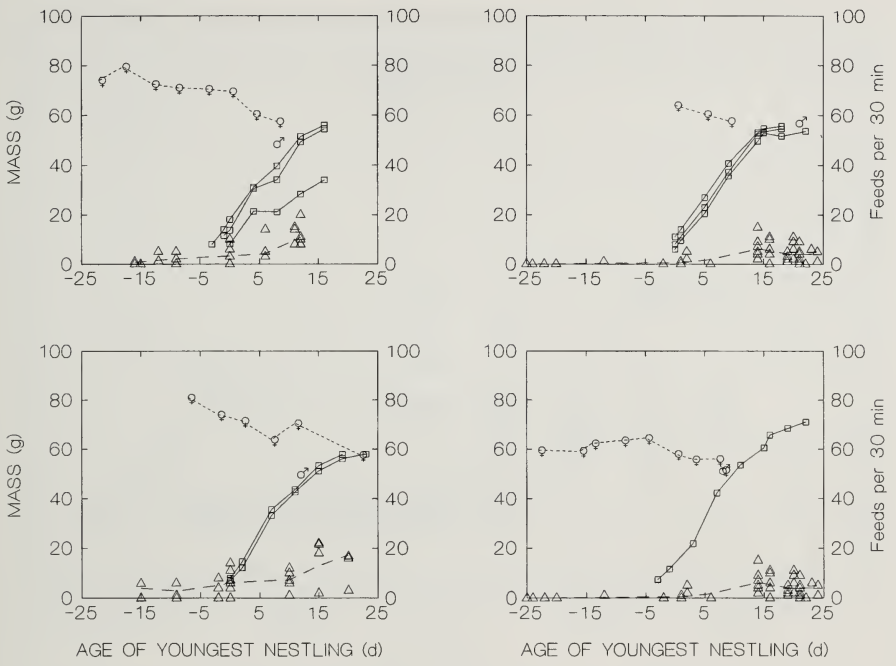

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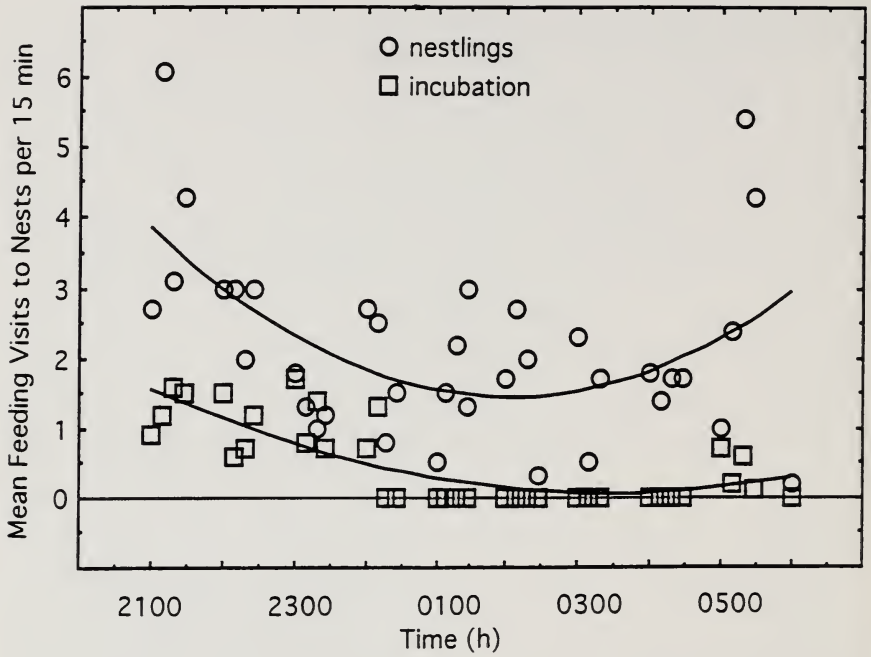

FIG. 2. Average feeding at four nests in 1983 during mid-incubation through the nestling period until the 25th day after hatching of the last egg. Data not collected at 00:30–03:00 h during incubation, when casual observations showed little or no activity (set at 0 for analysis but note actual 0 data). Bimodal patterns verified by 2° polynomial regressions ($r^2 > 0.30$, $P < 0.003$).

brood reduction, suggest that reduced productivity might be influenced by reduced parental feeding. Generally, feeding rates increased 10–15 days after the last chick hatched (Fig. 1).

Dusk and dawn peaks of feeding were evident (Fig. 2). Feeding per 15 min interval averaged 3.6 ± 1.3 at 21:30–23:30 and 05:30–06:30 h compared to only 1.6 ± 1.8 at 24:00–05:00 h ($F = 36.1$, $P < 0.001$). There was a marginally significant difference between the greater dusk and lesser dawn rates ($F = 4.0$, $P = 0.06$) and a pronounced difference between these peaks in the incubation and nestling periods ($F = 20.7$, $P < 0.001$, 2-way ANOVA; Fig. 2).

This bimodal pattern, typical of *Otus* at lower latitudes, also occurred in Flammulated Owls in Idaho (Hayward 1986). We figured an average of 81 (maximum 121) feeding trips per night during the nestling period, similar to Hayward's single-nest average of 73 over eight nights. Reynolds and Linkhart (1987b) did not watch dawn feeding, but their obser-

vations per 15 min in the first 4 h after sunset did not differ from ours ($F = 0.2$, ns), suggesting similar prey availability, and showed the same incubation versus nestling-period distinction ($F = 41.0$, $P < 0.001$; 2-way ANOVA).

Foraging and flying.—Flammulated Owls at CWG hunted in sit-and-wait fashion 3-50 m from their nests as Eastern Screech-Owls do. Thirty-seven straight-line forays to pine twig-tips (78%) or the ground (22%) resulted in at least 30 captures (81% success), very similar to the Eastern Screech-Owl's 83% success rate on insects. Identifiable prey were seven lepidopteran larvae and three small moths taken from pine foliage and a cricket caught on the ground at the edge of a grassy opening. Most foraging (78% of 81 perches) occurred along the interface between forest or woodland and grassland as in Oregon (Goggans 1986).

Adults arriving at nests with or without food often swooped up to the cavity from a 2–3 m flight path under or in the lower tree canopy and when departing tree cavities dived steeply and again flew low. This flight pattern was not seen in Colorado (R. Reynolds, pers. comm.). However, adults sometimes flew straight to a feeding perch and then to the cavity, as they did in Colorado, and the Eastern Screech-Owl displays both flight patterns.

DISCUSSION

Our study population at the lower edge of its local elevational range resembled the contemporaneous Colorado population located higher in elevation in conifer forest and also populations in Oregon (Goggans 1986) and British Columbia (Van Woudenberg 1992). Among the life history traits, reuse of nest cavities, foraging style, breeding mass decline, bimodal feeding, brood reduction, early fledging, and degree of hunting success characterize the Eastern Screech-Owl as well. Conversely, habitat type, breeding dispersal distance, nesting density, infrequent reuse of nest cavities, clutch-size, and nestling period are similar only among populations of Flammulated Owls.

Despite similarities, the CWG population exhibited productivity that was 0.8 fledglings per nest lower and a density flux 31–51% higher than in Colorado and Oregon. Also, site fidelity was somewhat lower as might be expected of a marginal locale. These and other differences suggest that the CWG population is cyclic and transient (high density flux, low site fidelity) because it is stressed (low female mass, low productivity) compared to the more stable population in central Colorado.

However, low productivity and high density flux are not unusual in *Otus*. Flammulated Owl productivities are like those of Eastern Screech-Owls in central Texas with 0.2–1.3 fledglings per breeding pair when

declining and 1.8–2.5 in the increase phase of population cycles. Also, that species' coefficients of annual density variation are 16–46%, resembling the 21–51% range of values in Flammulated Owls. By contrast, the much larger Tawny Owl (*Strix aluco*) produces 0.5–0.9 fledglings per pair with a density flux of only 5% (calculated from Southern 1970).

Research might have stressed our CWG population, but this seems unlikely in view of individuals renesting in the same cavities after disturbance caused abandonment (two cases). Moreover, the owls have been exposed to human activity for most of this century and are readily habituated. CWG was a lumber camp in the 1920s and, since then, has been used continuously as a children's summer camp. Rather than investigative biases, we believe that the CWG population is a natural sink, possibly supplied by a source population higher in the Zuni Mountains.

Spatial constraints are not evident at CWG, as nest cavities are in excess and territory size plus breeding dispersal are about the same as in Colorado. Also, food availability during incubation and nestling periods may not differ from that in Colorado, based on similar nest-provisioning rates, but could be reduced during courtship (production feeding), since the lighter-weight females at CWG laid fewer eggs per average clutch. While the kind of local stress is problematical, it may be related to food scarcity early in the nesting season.

Predation is a second possible limiting factor, contrastingly absent in the Colorado population (Reynolds and Linkhart 1987b). Known agents of failed nests at CWG were a gopher snake (*Pituophis melanoleucus*) that ate a clutch of eggs and an *Accipiter* sp. that consumed an adult. In addition, Abert's squirrels (*Sciurus aberti*) used at least two tree cavities used by Flammulated Owls and could be nest-site competitors if not predators. Symbiotic ants may be too infrequent to deter significant numbers of intruders.

Low productivity and high density flux also typified a predator-impacted population of Eastern Screech-Owls by contrast to a concurrently stable one in central Texas. There, arboreal snakes and mammals were the major predators in a situation resembling CWG by contrast to Colorado. Besides food supply and nest-site availability as regulatory factors in raptor populations (Newton 1991), predation may limit smaller species such as the *Otus* owls and should not be overlooked in future studies.

ACKNOWLEDGMENTS

Thomas Billings Jr., the late Hillis Howie, and the Cottonwood Gulch Foundation facilitated our studies over several decades. Laura Greffenius helped in the field. Robert Baldridge, Julian Watkins, and William Wheeler identified symbiotic ants in this and related studies. Brian Linkhart, Richard Reynolds, and Jeffrey Roberts commented on the manuscript, which was supported in preparation by the USDA Forest Service.

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Wilson Bull., 107(3), 1995, pp. 538–542

SHORT COMMUNICATIONS

The effects of exogenous testosterone on male Northern Mockingbirds during the breeding season.—The challenge hypothesis (Wingfield et al. 1990) states that a positive correlation between plasma testosterone (T) and aggression occurs only under conditions of social instability, that is, when access to resources is being persistently challenged in contests over territory borders or position in a dominance hierarchy. Sizeable increases in plasma T levels above a relatively low breeding-season baseline are produced by intermale aggression and female sexual activity, while male parental care is associated with lower T levels. The hypothesis accounts for fluctuations in breeding-season levels of plasma T in numerous temperate avian species (Wingfield et al. 1990).

Northern Mockingbirds (*Mimus polyglottos polyglottos*) in the southeastern United States aggressively defend all-purpose territories year-round against conspecific intruders and male T levels fluctuate substantially across the breeding season (Logan and Wingfield 1995). However, recent work has failed to establish a connection between heightened aggression and elevations in plasma T in mockingbirds. Specifically, Logan and Carlin (1991) showed that exogenous T administered in autumn stimulated reproductive behavior such as song, mate acquisition, and nest building. Territorial behavior, however, was either unaffected or inhibited, even though territorial interactions normally peak in autumn in mockingbirds. When mockingbirds were trapped periodically for blood samples during the breeding season, mated males' T levels peaked during early nest building and remained low later in the season despite continued maintenance of the territory and the female. Unmated males defending spring territories showed T levels below the peak seen in mated males (Logan and Wingfield 1995). These data raise the possibility that T may not be related to intermale aggression during the breeding season in mockingbirds. The purpose of this study was to examine experimentally the impact of exogenous T on breeding-season territorial aggression in male mockingbirds. If the challenge hypothesis applies, the frequency of territorial aggression should increase in T-implanted males, and consequently, neighbors of T-implanted males should show elevated plasma levels of T.

Methods.—Using the procedures described in Logan and Carlin (1991), four color-banded male mockingbirds residing on campus at the University of North Carolina at Greensboro were implanted with sealed 20 mm lengths of Silastic tubing packed with crystalline T (T-implanted birds) between 10 March and 1 July 1992. Four color-banded control males holding territories on campus similarly were implanted with empty implants (C-implanted birds) between 27 February and 14 April of the same year. Prior work indicates that the T implants elevate plasma T levels to approximately 10.3 ± 4.9 ng/ml (Logan and Carlin 1991). In each group there were three unmated and one mated bird, each bird having one to three territorial neighbors. When captured and implanted, the T-implanted mated bird had a nest with one egg, and the C-implanted mated bird had just acquired a mate.

A mean of 12 (range 6–20) 15-min focal-animal behavior samples were taken on each of the C-implanted birds and T-implanted birds from mid-March through mid-July. Behavior sampling typically began several days after implantation. In addition, a mean of seven (range 2–16) 15-min samples were also taken on each of 10 unimplanted, color-banded males whose territories bordered those of the implanted birds. Those birds whose territories bordered a T-implanted bird will be referred to as "T neighbors" (N = 5); territories of "C neighbors" (N = 5) bordered the territory of a C-implanted bird. Upon capture, 300–400 μl of blood was collected from C neighbors and T neighbors. Plasma steroid hormone

concentrations were determined via radioimmunoassay at the University of Washington according to the methods of Wingfield and Farner (1975).

We tested whether aggression levels were influenced by T implants by comparing conspecific territorial chases and the production of "hew" calls in T- versus C-implanted birds. In the neighbors of implanted birds, we examined whether territory size decreased due to the expansion of the territory owned by the neighboring implanted bird. Territory size, which was measured for most birds, was assessed using the method described by Odum and Kuenzler (1955). Other measures included overall activity levels and time spent in song. Song was not included as a measure of territorial aggression because previous studies have suggested that male mockingbirds use song primarily for mate attraction (Logan and Carlin 1991, Merritt 1985). Time-out time was recorded when all visual and acoustical contact with the focal bird was lost. The mean ratio of time-out time to total time sampled was 0.162 for T-implanted birds, 0.120 for C-implanted birds, 0.148 for T neighbors, and 0.117 for C neighbors (Kruskal-Wallis $H = 1$, $P > 0.30$)

Nonparametric statistics were used in all analyses. Each individual bird's mean across focal samples was used to calculate the group means. Two-tailed tests were used unless the experimental hypothesis specified a particular direction for between-group differences, in which case a one-tailed test was used.

Results.—T-implanted birds were not greater than C-implanted birds in the average number of territorial chases per 15 min. The mean ± SE average number of territorial chases per 15 min was 0.047 ± 0.05 for T-implanted birds and 0.104 ± 0.036 for C-implanted birds (one-tailed Mann-Whitney $U = 5$, $P > 0.20$). Also, T-implanted birds were not greater than C-implanted birds in the percentage of 15-min samples during which one or more territorial chases were recorded. The mean ± SE was 4.69 ± 4.7% for T-implanted birds and 8.15 ± 3.59% for C-implanted birds (one-tailed $U = 5$, $P > 0.20$). Further, T-implanted birds did not produce more "hew" calls than C-implanted birds. The mean ± SE number of "hews" per min of time-in time was 0.047 ± 0.031 "hews" for T-implanted birds and 0.026 ± 0.022 hews for C-implanted birds (one-tailed $U = 6$, $P > 0.30$). T-implanted birds differed from C-implanted birds in territory size. Mean ± SE territory size was 1.48 ± 0.18 ha for N = 4 T-implanted birds and 0.503 ± 0.17 ha for N = 3 C-implanted birds (two-tailed $U = 0$, $P = 0.056$; territory size data were not available for the mated C-implanted bird). Similar effects of T on spatial behavior have been reported in Dark-eyed Juncos (*Junco hyemalis,* Chandler et al. 1994). However, none of the T-implanted birds annexed part or all of another bird's territory. That is, the territory gains of T-implanted birds did not come at the expense of neighbors. Rather, T-implanted birds expanded their territories into adjacent unoccupied areas, stopping when they reached a defended area. Subsequently they used both the older and newly acquired space. In contrast, one C-implanted bird had a large, unoccupied, and apparently suitable area adjacent to his territory which he was never observed using. Another C-implanted bird, apparently shifting his territory, was consistently seen in an area west of that which he occupied in the previous sample, but was never seen using the area from which he expanded.

Because exogenous testosterone increases song in the fall in this species, it was predicted that T-implanted birds would sing more than C-implanted birds in the spring as well. Initial comparisons showed no differences between groups in the amount of song produced per 15 min. However, because increases in song produced by exogenous T in autumn can be inhibited by the presence of a female, song production was reanalyzed after eliminating the mated male from each group. Unmated T-implanted birds sang more than unmated C-implanted birds: the mean ± SE number of 15-sec intervals with song per 15 min was 24.34 ± 1.65 for the three T-implanted birds and 8.44 ± 3.0 for the three C-implanted birds (one-tailed $U = 0$, $P = 0.05$).

T also increased overall activity levels. For each bird, the total number of perch changes across all samples was divided by the total number of minutes of time-in time. The mean ± SE number of perch changes per min of time-in time was 0.640 ± 0.093 for T-implanted birds and 0.351 ± 0.063 for C-implanted birds (two-tailed $U = 0$, $P = 0.014$).

The challenge hypothesis predicts that neighbors of T-implanted birds (T neighbors) would have higher levels of plasma T than neighbors of C-implanted birds (C neighbors) if the T-implanted birds were aggressively challenging their neighbors. Two T neighbors were trapped; their plasma T titres equalled 1.19 ng/ml and 0.91 ng/ml. To increase the sample size for the comparison group, four neighbors of unimplanted males were combined with three neighbors of C-implanted males; the mean ± SE plasma T titres in these seven birds was 1.06 ± 0.24 ng/ml. T neighbors were not greater than C neighbors (one-tailed $U = 6$, $P > 0.30$).

Using those birds for which territory size data were available, three T neighbors did not differ in territory size from four C neighbors (two-tailed $U = 3$, $P > 0.20$). Using all birds, T neighbors (N = 5) did not differ from C neighbors (N = 5) in the percentage of 15-min samples with territorial chases (two-tailed $U = 11$, $P > 0.30$), mean number of territorial chases per 15 min (two-tailed $U = 10$, $P > 0.30$), mean time in song (two-tailed $U = 6$, $P > 0.20$), or average activity levels (two-tailed $U = 12$, $P > 0.30$). T neighbors differed from C neighbors in the production of hew calls per 15 min in that T neighbors produced more hew calls (two-tailed $U = 1$, $P = 0.02$). However, hew calls are used in a variety of aggressive contexts, including nest defense against predators (Breitwisch 1988). Four of five T neighbors had eggs or young during sampling, whereas only one of five C neighbors had eggs or young. Thus, this result may be due to phase in the breeding cycle rather than T-induced aggression in implanted birds.

Discussion.—T implants are known to enhance territorial aggression in several avian species. For example, male Red-winged Blackbirds (*Agelaius phoeniceus*) show enhanced territorial aggressiveness following T implantation (Beletsky et al. 1990). The impact of T was apparent in the behavior of the T-implanted mockingbirds: they were more active and increased their territory size, and unmated males sang more than controls. However, the measured aggressive behaviors were not affected by T implants, and the changed behavior in the T-implanted birds appeared to have no impact, hormonal or behavioral, on their neighbors.

It is possible that the results reported here are due to the small sample sizes used. However, in other species of birds, exogenous T has had large effects on the behavior of other species. For example, T implants induced polygyny in normally monogamous White-crowned Sparrows (*Zonotrichia leucophrys*), and T-implanted birds' territory sizes averaged more than twice that of controls (Wingfield 1984). In Red-winged Blackbirds (*Agelaius phoeniceus*), T implants more than doubled both the mean frequency of attacks and the song rate (Searcy and Wingfield 1980). In mockingbirds, the effects of T on other behaviors were large enough to be detected, in most cases, with sample sizes of three. Therefore, it is unlikely that the lack of relationship between T and territorial aggression in mockingbirds resulted solely from the small sample sizes.

If most territorial chases occur as a result of intruders entering the territory and being chased out, then the lack of differences in territorial aggression found here may reflect a lack of a difference in intruder pressure on T-versus C-implanted birds; that is, it is possible that the groups did not differ in territorial chase rate because they did not differ in the rate of intrusions onto their territories. However, if exogenous T did elevate aggressive behavior, it is likely that T-implanted birds would have initiated aggressive interactions with their neighbors, which would have resulted in between-group differences in territorial interaction frequency.

Researchers have found that T in breeding birds fails to produce conspecific aggression in two different circumstances. First, many tropical species show either very low levels of T during periods of territorial activity or greatly reduced fluctuations in T compared to temperate species (see summary in Levin and Wingfield 1992), though a greater sensitivity to T in tropical species has not been ruled out. The current range of the Northern mockingbird and other *Mimus* species extends into the tropical zone, and bird counts and anecdotal evidence have charted a northward expansion of the Northern mockingbird (Derrickson and Breitwisch 1992). It is therefore possible that the relationship between T and behavior in *M. polyglottos* was influenced by tropical conditions at some point in the species' phylogeny. Thus, the results presented here could be viewed as consistent with current data on T levels in tropical avian species, to which the challenge hypothesis does not apply.

Second, it appears that the effects of T on aggressive behavior can be dampened under highly stable social conditions, such as being housed with familiar individuals (Archawaranon et al. 1991) or perennial territoriality (Wingfield and Hahn 1994). Levin and Wingfield (1992) have argued that the association between T and territorial aggression seen in several temperate migratory species may be extremely metabolically costly in temperate species that defend territories year-round. Wingfield and Hahn (1994) found that simulated territorial intrusions produced a significant increase in plasma T in migratory White-crowned Sparrows, but no significant plasma T increase in sedentary Song Sparrows (*Melospiza melodia*), despite strong behavioral reactions in both species. Though some effects of T may be present early in the season in Song Sparrows, particularly in high-density populations, they suggest that aggressive behaviors that are T-dependent in migratory species may not require high T levels in species or populations that defend territories year-round. As most mockingbird populations in the southeast are perennially territorial, this metabolic constraint may apply. Specifically, it may be too energetically costly for mockingbirds to link aggressive behavior to the production of hormones when the aggressive maintenance of a territory is required year-round. Also, perennial territoriality may lead to stable social conditions (due to familiarity with neighbors) which, despite hormonal state, inhibit or fail to stimulate aggressive behavior (Archawaranon et al. 1991). Thus, the combination of perennial territoriality and social inertia may account for the ineffectiveness of T in altering spring territorial aggression in mockingbirds.

Acknowledgments.—Sigma Xi, The Scientific Research Society and the University of North Carolina Research Council financially supported this research. We thank John Wingfield and Lynn Erckmann for performing the radioimmunoassays, Jeffrey Patton for providing the planimeter, and C. Ray Chandler, Randall Breitwisch, and Charles Blem for their helpful comments which greatly improved the manuscript.

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Wilson Bull., 107(3), 1995, pp. 542–547

Effects of food supplementation and predator simulation on nuthatches and parids within mixed-species flocks.—Although many ornithologists have studied mixed-species flocks, few have examined spatial positioning of birds within flocks. Flocks, here defined as three or more birds that move together as a group, vary from loose associations of individuals separated by tens of meters to tight clusters of birds only centimeters apart. Variations in spacing are interesting because they may either enhance or reduce the benefits that birds acquire by flocking. For example, birds that are farther apart may have more difficulty acquiring information about food or predators from each other but may have reduced costs due to fewer aggressive interactions. Thus, spacing within flocks may reflect a balance between attractive and repulsive forces between flock members (Emlen 1952). Distances between flock members are likely to change over time scales of minutes or hours as attractive and repulsive forces vary with changes in flock size and composition (Caraco and Bayham 1982, Pearson 1989), energy reserves of flock members, or environmental factors such as habitat structure, food availability, and predation pressure (Grzybowski 1983, Prescott 1987, Pearson 1991). In this paper I examine spacing among Brown-headed Nuthatches (*Sitta pusilla*), Carolina Chickadees (*Parus carolinensis*), and Tufted Titmice (*P. bicolor*) within heterospecific flocks. The basic goal was to determine whether distances between birds varied either as food availability varied or as apparent threat of predation

varied. Three hypotheses were tested by experimentally varying food availability and apparent predator abundance. These are: (1) Nuthatches and chickadees flock less closely when these species have less overlap in their food resources; (2) Nuthatches and parids flock less closely when food is easily obtained by both species; and (3) Nuthatches and parids flock more closely when there is a relatively high likelihood of encountering a predator.

Methods.—Brown-headed Nuthatches in the present study frequently foraged on cones and on the bark of loblolly pines (*Pinus taeda*) and shortleaf pines (*P. echinada*). They typically were encountered in pairs or tight conspecific flocks of up to seven nuthatches, which were usually part of heterospecific flocks that often included chickadees, titmice, and several species of woodpeckers, kinglets, and warblers (Yaukey, unpubl. data). Parids are thought to form the nuclei of these flocks (Morse 1967, 1970). Both parids foraged in deciduous and coniferous trees at various heights; chickadees used pine cones, but not as often as nuthatches (Yaukey, pers. obser.).

Two study sites 2.7 km apart were selected in the State Botanical Garden of Georgia, and in Whitehall Forest of the Univ. of Georgia, (33°56′N, 83°24′W), near Athens, Georgia. Although these sites were not randomly selected, they were typical of habitat conditions common in the piedmont region of northern Georgia. Sites were chosen because they contained nuthatches and parids, were dominated by pines >9 m tall, and contained no human habitations or bird feeders. Both sites were extensively wooded and dominated by pines but contained roads or powerlines; the Botanical Garden had two clearings, one of which held several greenhouses. The number of different nuthatches using each site was not precisely calculated but varied daily (or hourly) from approximately two to five at the Botanical Garden and from six to twelve at Whitehall. I collected data from November to February during two winters (1989–1990, 1990–1991) at all hours of the day.

To measure distances between nuthatches and parids, I followed a flock of nuthatches (or a lone individual) and at 10-min intervals I paced the distance from the most easily visible nuthatch in the flock to the first chickadee detected. In most cases, this appeared to be the chickadee closest to the nuthatch, and highly active or vocal chickadees were probably represented more than inconspicuous ones. The birds were typically >5 m above the ground and appeared not to be alarmed by the observer. If no parids were present within 50 m, the nuthatch was recorded as not being flocked with chickadees. The same procedure was also followed to measure the distance to the first titmouse detected. In the first winter, a nuthatch was recorded only to be "not-flocked" with parids after 10 min elapsed without a parid being detected. To examine whether observations taken 10 min apart were autocorrelated, Durbin-Watson statistics (SAS Institute 1989) were calculated for these distance data from regressions (Yaukey 1991); with a few exceptions (indicated below), d values were all ≥1.78, indicating that there was little or no temporal autocorrelation in distance observations. I also regressed interspecific distance measurements of these species onto air temperature, wind speed, solar radiation, time of day, and date, and found few significant relationships (Yaukey 1991). Consequently, weather and time variables are omitted from the present analyses.

During the winter of 1989–1990, an experimental treatment was conducted at each site in November, followed by a non-treatment period in December, and another treatment in January. In 1990–1991, the non-treatment period at each site extended into January, and the second treatment into early February. At least 15 days elapsed between treatments and subsequent non-treatment periods. The distances between nuthatches and each parid species were compared between each treatment period and the non-treatment period at the same site in the same winter using one-tailed *t*-tests. Because data may have violated assumptions of *t*-tests in some cases, the proportion of nuthatches that flocked with either chickadees or titmice (within 50 m) was also compared using nonparametric chi-square tests with Yate's

correction (Zar 1984). The experimental design enabled treatments and non-treatments to be compared at the same site, but did not allow them to be conducted simultaneously. Although it is also possible that birds became habituated to treatments or to the observer, or that effects of treatments lingered into nontreatment periods, such effects were not evident.

The hypothesis that nuthatches and chickadees flock less closely when these species used increasingly different food resources was tested by attracting chickadees to feeders that nuthatches could not use. Sunflower seed was provided in plastic 3.7-L milk jugs bent so that they could be entered only on the wing from directly below. Jugs were hung separately in trees, at heights that ranged from about 1–9 m, at six feeding stations spread evenly across the core area of the site. During this experiment chickadees used these feeders heavily, while nuthatches did not use them, thus decreasing the overlap of their diets. If either species had been following the other closely to learn of food resources that the other species located, it should have followed less closely during the experimental treatment. Therefore, distances between chickadees and nuthatches were predicted to increase when food was provided. This treatment was conducted only at the Botanical Garden in November 1989.

The hypothesis that nuthatches flock less closely with either chickadees or titmice when food was easily obtained by both nuthatches and parids was tested by providing food for all species following a protocol similar to that used by Berner and Grubb (1985) and Grubb (1987). Sunflower seed was provided in modified plastic 3.7-L milk jugs that all species could enter through holes in their sides. Feeders were hung in groups of three, approximately 5–9 m high in trees, in three places evenly distributed in the core area of the site. Distance measurements were not collected if both the nuthatch and parid were within 10 m of a feeder that both species were using. If nuthatches had been following either parid (or vice versa) closely to acquire information about food resources by watching the other species, they should have moved apart when they were provided with food, because they did not need to rely on the other species as much. The distance between them was predicted to increase when they received supplementary food. This treatment was conducted only at Whitehall in January 1990.

The hypothesis that nuthatches would flock more closely with parids when they sensed a high likelihood of encountering a predator was tested by playing taped Sharp-shinned Hawk (*Accipiter striatus*) calls (Cornell Laboratory of Ornithology 1971). This technique was meant to simulate the presence of a hawk in the immediate vicinity rather than an actual attack. During periods of data collection, a tape of continuous hawk calls 48 sec in length was played at arbitrarily selected times spaced at irregular intervals but averaging approximately once per hour and beginning before the first observation. At Whitehall, I also played the tape whenever I switched to observing a new flock of nuthatches. The tape was played on a portable cassette recorder at 10–40 m distance from the closest nuthatch. During November 1989, the cassette recorder was hand held; subsequently, it was hung from a tree limb within 2.5 m of the ground, and I usually stood at least 10 m from it. If nuthatches and parids flocked more closely when they were more likely to encounter a predator, distances between them should have decreased when the presence of a predator was simulated. This treatment was conducted six times: at Whitehall in November 1989, at the Botanical Garden in January 1990, and at both sites in November 1990 and Jan.–Feb. 1991.

Results.—Addition of feeding stations that could be used only by chickadees had no influence on the distances between nuthatches and chickadees within flocks or on the proportion of nuthatches that flocked with chickadees (Table 1). Neither did providing food for all species affect the distances between nuthatches and chickadees within flocks or the proportion of nuthatches that flocked with chickadees (Table 1).

Addition of food that could be used only by chickadees did not affect distances between

TABLE 1

DISTANCES BETWEEN NUTHATCHES AND PARIDS WITHIN FLOCKS, AND PERCENTAGE OF NUTHATCHES THAT FLOCKED WITH PARIDS, WHEN FOOD WAS PROVIDED (FOOD), COMPARED TO NON-TREATMENT (N-T) PERIODS

		N		Mean distance (m)				Percent in flock			
Site[a]	Year	Food	N-T	Food	N-T	t	P[b]	Food	N-T	χ^2	P
Nuthatch-chickadee interactions											
BG	Nov 89	91[c]	90	14.0	14.3	0.13	NS	96.7	93.3	0.49	NS
WF	Jan 90	80[d]	102	20.2	19.2	−0.49	NS	81.3	79.4	0.01	NS
Nuthatch-titmouse interactions											
BG	Nov 89	85[c]	83	20.3	19.2	−0.39	NS	63.5	39.8	8.58	**
WF	Jan 90	79[d]	97	24.6	18.8	−2.25	*	54.4	52.6	0.01	NS

[a] BG: Botanical Garden, WF: Whitehall Forest.
[b] *: $P < 0.02$; **: $P < 0.01$.
[c] Treatment: food provided for chickadees.
[d] Treatment: food provided for all species.

flocked nuthatches and titmice. However, a higher proportion of the nuthatches were found flocked with titmice when food was provided for chickadees (Table 1). Flocked nuthatches and titmice were significantly farther apart when food was provided for all species as predicted (Table 1). The proportion of nuthatches that were flocked with titmice did not change when all species were provided with food.

Nuthatches were significantly closer to chickadees within flocks when predators were simulated at the Botanical Garden in January 1990 and at Whitehall in November 1990 than in their respective non-treatment periods (Table 2). However, the significance of the Botanical Garden experiment may have been overestimated, as the data showed evidence of serial autocorrelation. Three of the remaining four replicates showed some (nonsignificant) increase in the number of nuthatches observed within 5 m of a chickadee when hawk calls were played. Despite these patterns, *fewer* nuthatches were found flocked with chickadees at Whitehall in November 1990 and January 1991 and at the Botanical Garden in November 1990 than during their December non-treatment periods (two-tailed χ^2 tests, Table 2). This pattern was evident (but nonsignificant) in two of the other three predator simulation replicates. Thus, predator simulations appeared to stimulate two different responses from the birds: in some cases, nuthatches and chickadees became more tightly grouped and in others they ceased to flock together. Often, both responses were evident during the same treatment; however, neither response was particularly strong or consistent.

The proximity of nuthatches to titmice was not influenced as strongly by playing hawk calls as was the proximity of nuthatches to chickadees (Table 2). No simulations produced significant decreases in distances between birds within flocks. However, four replicates showed significant decreases in the proportion of nuthatches that were flocked with titmice. The significant results in two-tailed tests occurred at both the Botanical Garden and Whitehall during both November 1990 and January 1991 (Table 2). This pattern was also present but nonsignificant in the two other predator simulations. Thus, nuthatches and titmice appeared to move apart on several occasions, when hawk calls were played.

Discussion.—The inability of providing food, either for chickadees or for all species, to affect the distances between nuthatches and chickadees in this study suggests that inter-bird

Table 2

Distances between Nuthatches and Parids within Flocks, and Percentage of Nuthatches that Flocked with Parids, when Hawk Calls were Played (Hawk), Compared to Non-treatment Periods (N-T)

		N		Mean distance (m)				Percent in flock			
Site[a]	Year	Hawk	N-T	Hawk	N-T	*t*	*P*[b]	Hawk	N-T	χ^2	*P*
Nuthatch-chickadee interactions											
WF	Nov 89	89	102	16.4	19.2	1.39	NS	83.1	79.4	0.22	NS
BG	Jan 90	82	90	10.8	14.3	2.04[c]	*	84.1	93.3	2.81	NS
WF	Nov 90	73	91	10.4	16.2	2.71	***	64.4	86.8	10.22	***
WF	Jan 91	61	91	21.6	16.2	−1.60	NS	26.2	86.8	54.64	****
BG	Nov 90	75	77	11.3	12.7	0.69	NS	68.0	85.7	5.76	**
BG	Jan 91	59	77	12.1	12.7	0.30	NS	81.4	85.7	0.20	NS
Nuthatch-titmouse interactions											
WF	Nov 89	81	97	19.8	18.8	−0.37	NS	46.9	52.6	0.36	NS
BG	Jan 90	74	83	16.9	19.2	0.71	NS	36.5	39.8	0.07	NS
WF	Nov 90	66	75	20.6	16.3	−1.59	NS	39.4	76.0	17.95	****
WF	Jan 91	56	75	27.5	16.3	−2.47[c]	NS	23.2	76.0	33.81	****
BG	Nov 90	80	67	16.0	12.0	−0.56	NS	3.8	40.3	27.78	****
BG	Jan 91	56	67	10.2	12.0	0.41	NS	16.1	40.3	7.52	***

[a] BG: Botanical Garden, WF: Whitehall Forest.
[b] *: $P < 0.05$; **: $P < 0.02$, ***: $P < 0.01$, ****: $P < 0.001$, NS: nonsignificant.
[c] *t* calculated assuming unequal variances; all other *t*'s assume equal variances.

distances were not determined by birds attempting to watch each other foraging. Although other food-supplementation studies have indicated that mixed flock participants gain some foraging benefit by flocking (Berner and Grubb 1985, Grubb 1987, Szekely et. al. 1989), these studies did not determine that the species involved watched each other to locate food. Although nuthatches and titmice did move apart when food was provided, this result should be treated with caution until it is replicated and the mechanisms are identified.

When nuthatches and chickadees were exposed to hawk calls in this study, they appeared to draw close together in some cases but to cease flocking together in others. The latter trend was also observed between nuthatches and titmice. The appearance of both flock tightening and departure from the flock in different cases raises the possibility that each action may be preferable under particular circumstances but that remaining loosely flocked might be less desirable. Although flock tightening could occur because birds converge on a single area of cover when confronted with a predator, such converging movements were not detected in the field. Most of the mechanisms that have been hypothesized to reduce the risk of predation in flocks probably are maximally effective in tight group situations. For instance, animals should group tightly to reduce risk of being singled out as prey (Hamilton 1971). Although vocal alarm responses are audible at a distance, birds that give alarms may not detect a predator until it is already upon other flock members, if those members are tens of meters away. On the other hand, flocks themselves may attract predators because they are more noisy and visible than individual birds. It is possible that the maximum risk of predation actually occurs for birds that are loosely attached to a flock and may encounter a predator attracted to the flock but derive minimal benefit from other flock

members in avoiding capture. Thus, birds that perceive a risk of predation might either leave the flock or draw close to other members but avoid being *loosely* associated with the flock.

Acknowledgments.—This study fulfilled part of the Ph.D. requirements at the Univ. of Georgia. I thank my adviser, Kathleen Parker, and committee members David Butler, Vernon Meentemeyer, Albert Parker, and H. Ronald Pulliam. Steven Rathbun, Ronald Mitchelson, and Kermit Hutcheson offered helpful statistical advice, and John B. Dunning, Jr., Michael L. Morrison and an anonymous reviewer offered helpful comments. The State Botanical Garden of Georgia and School of Forest Resources at the Univ. of Georgia allowed me access to their properties.

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Wilson Bull., 107(3), 1995, pp. 548–551

Mallard-like ducks in the Playa Lakes Region.—The relationship of the Mallard (*Anas platyrhynchos* L.) to similar members of the genus *Anas* is often complex (Johnsgard 1961). Hybridization of Mallards with American Black Ducks (*A. rubripes* Brewster), Mottled Ducks (*A. fulvigula maculosa* S.), and Mexican Ducks (*A. diazi* R.), further complicates taxonomic status and identification of subgroups within the Mallard complex. Experimental crosses and back crosses of Anatini result in a broad range of overlapping phenotypes (Phillips 1915, 1921). Furthermore, subgroups within the Mallard complex are often difficult to differentiate using biochemical methods (Ankney et al. 1986, Hitchmough et al. 1990). Thus, for wild monomorphic hybrids within the Mallard complex, it may be difficult at best to determine the taxonomic status of both parental types based on plumage characteristics or biochemical analysis and nearly impossible to determine in which F_i generation the bird belongs.

The Playa Lakes Region (PLR) in the Southern Great Plains represents a major wintering area for waterfowl in the Central Flyway. At least 14 species of ducks occur on the PLR. However, few Mallard-like ducks have been reported. Oberholser (1974a) reported a Mexican Duck collected in Swisher County, Texas and a sight record in Randall County, Texas. However, Hubbard (1977) believed that both were probably Mottled Ducks and he suggested that reports of Mexican Ducks in Colorado and Nebraska were most likely hybrids between Mallards and Black Ducks or Mallards and Mottled Ducks. Although Mottled Ducks have been considered a coastal species, they have been found in Oklahoma (Sutton 1971), Kansas (McHenry 1968), Nebraska (Silcock et al. 1986), northeast Texas, Iowa, and Wisconsin (Stutzenbaker 1988). These reports suggest extensive inland movements by at least some individuals from traditionally non-migratory Mottled Duck and Mexican Duck populations.

Due to the paucity of information concerning Mallard-like ducks on the PLR, we report two sight and four specimen records. Where possible, physical measurements of body mass, body length, and wing length of the specimens were compared to male Mallards collected during the same periods. In addition, maximum length, width, and height of the culmen, and the length of the tarsus and middle toe were measured for three specimens.

A male duck resembling a female Mallard was shot 3 November 1984 on a playa lake in Castro County, Texas (34°24′N, 102°15′W); the specimen was thought to be either a Mottled Duck or Mexican Duck (P. N. Gray, pers. comm.). During waterfowl trapping operations (Fedynich et al. 1989) on 26 January 1986 in Parmer County, Texas (34°28′N, 102°55′W), a female Black Duck was captured, photographed, and released. Apparently,

TABLE 1

COMPARATIVE MEASUREMENTS OF MALLARD-LIKE DUCKS WITH MALLARDS COLLECTED IN THE PLAYA LAKES REGION OF TEXAS

					Mallard		
Measurement[a]	Specimen 1	Specimen 2	Specimen 3	Specimen 4	N	$\bar{x}$	SE
Mass	1129	1200	1338	1224	257	1248	8.1
Wing-chord length	289	240[b]	285	278	258	291	0.6
Total body length[c]	459	475[b]	460	—	204	501	1.3

[a] Mass in g, lengths in mm.
[b] Values from museum prepared specimen; wing could not be fully extended.
[c] Measured from tip of bill to base of tail feathers.

TABLE 2
SELECTED MEASUREMENTS OF MALLARD-LIKE DUCKS COLLECTED ON THE PLAYA LAKES REGION OF TEXAS

Measurement[a]	Specimen 2	Specimen 3	Specimen 4
Hubbard index value[b]	30	32	25
Exposed culmen length	55	58	57
Culmen nail to nostril	41	45	42
Maximum culmen height	22	20	25
Maximum culmen width	22	22	24
Middle toe length	56	56	54
Tarsus length	41	44	47

[a] Lengths in mm.
[b] Values can range from 0 for phenotypically "pure" Mallard to 36 for phenotypically "pure" Mexican Duck.

this is a new locality record for this species. A male duck with traits resembling those of a Mexican Duck, was collected 26 October 1988 by O. E. Rhodes, Jr. on a playa lake in Parmer County, Texas (34°31′N, 102°46′W); rudimentary measurements were made (Table 1, specimen 1) before its inadvertent loss. Another male (specimen 2), found in the waterfowl collection at the Texas Tech Museum, was cataloged as a Mexican Duck. It was collected on 6 December 1980 by L. W. Robbins in Castro County, Texas (collection number TTU 4158). Specimen 3, a male duck resembling a Mexican Duck, was collected on 30 November 1988, on a playa in Castro County, Texas (34°30′N, 102°20′W) by O. E. Rhodes, Jr. Another male (specimen 4) resembling a Mexican Duck was collected 16 January 1990 by A. M. Fedynich on a tailwater irrigation pit in Castro County, Texas (34°26′N, 102°04′W). Specimens 3 and 4 were deposited in the Texas Tech Museum, Lubbock, Texas (TTU 4224 and 4225).

Plumages of specimens 2 and 3 appeared consistent with descriptions of Mexican Ducks (Palmer 1976a, Hubbard 1977). However, specimen 4 most closely resembled the description by Oberholser (1974a) of the Northern Mexican Duck (*A. diazi novimexicana*), which is now synonymized as *A. platyrhynchos diazi*. Hubbard (1977) index values for specimens 2, 3, and 4 were similar to those of Mallard × Mexican Duck hybrids (Table 2). However, since the Hubbard index generally weights plumage coloration by how dusky a bird is, it may not differentiate between Mottled or Mexican Ducks. It is possible that specimens designated by the Hubbard index as Mallard × Mexican Duck hybrids could also be Mallard × Mottled Duck hybrids.

Obvious differences between specimens 2, 3, and 4 and a phenotypically pure male Mallard (alternate plumage) included the overall female Mallard-like coloration, absence of a green head and white neck collar, presence of a dark eye stripe, and fuscous lesser and middle coverts with light brown edging. In each of our specimens the greater coverts had prominent subterminal white and terminal black banding and the secondaries had subterminal black and terminal white banding, which precluded them from being either a Black Duck or Mottled Duck. However, because of the wide range of plumage variation found in Mallard × Black Duck and Mallard × Mottled Duck hybrids (Phillips 1915, 1921), we cannot discount the possibility of hybrid combinations, even though plumage characteristics (excepting the 2 white speculum bars) of male Mallards were absent.

Specimen measurements (Tables 1 and 2) were generally within the ranges reported for Mexican Ducks (Oberholser 1974a, Hubbard 1977, Scott and Reynolds 1984) and Mottled

Ducks (Oberholser 1974b, Palmer 1976b, Stutzenbaker 1988). However, our specimens tended to be heavier than sample averages of Mottled Ducks from coastal Texas (Stutzenbaker 1988) and Florida (Palmer 1976b), and were more similar to Mallards collected on the PLR (Table 1). This may have been the result of seasonal fat deposition, which occurs in Mallards overwintering on the PLR (Whyte et al. 1986).

Four of the Mallard-like ducks were shot during field collections for Mallards and were initially thought to be hen Mallards before in-hand inspection. The ratio of these ducks to phenotypically normal Mallards (males and females) collected during winters 1984–1990 was 4:673 (0.6%). Comparisons with only female Mallards yielded a ratio of 4:206 (1.9%). These results suggest that more Mallard-like ducks occur in the PLR than previously thought. The relatively low numbers of monomorphic Mallard-like ducks collected on the PLR most likely result from their similarity to hen Mallards, which are de-emphasized in current hunting regulations.

Acknowledgments.—We thank P. N. Gray for allowing use of his Mallard data. Funding was provided by the Dept. of Range and Wildlife Management, Texas Tech Univ., and by contract (DE-AC079-76SR00-819) from the U.S. Dept. of Energy to the Univ. of Georgia's Savannah River Ecology Laboratory.

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Wilson Bull., 107(3), 1995, pp. 551–555

First description of the nest and eggs of the Socorro Mockingbird.—The Socorro Mockingbird (*Mimodes graysoni*) represents a monotypic genus endemic to Isla Socorro, Mexico (Brattstrom and Howell 1956). Formerly abundant on Socorro, this species has declined since the middle of this century (Jehl and Parkes 1982) and now numbers between approximately 100 (Castellanos and Rodríguez-Estrella 1993) and 300 individuals. As a consequence of its restricted range and small population size, *Mimodes* is considered critically endangered (Collar et al. 1992). Possible causes of the species' decline include predation from feral cats, habitat destruction caused by feral sheep, and competition with recently arrived Northern Mockingbirds (*Mimus polyglottos*) (Jehl and Parkes 1982). Determining what action is needed to prevent the extinction of *Mimodes* will require understanding of the species' breeding biology. However, almost nothing of this bird's natural history is known. Here we present the first description of the nests and eggs of the Socorro Mockingbird, along with preliminary observations about breeding seasonality and behavior derived from our ongoing field study of the conservation status of *Mimodes graysoni.*

Isla Socorro lies 460 km SSW of Cabo San Lucas, Baja California Sur, and 580 km west of Cabo Corrientes, on the Mexican mainland. Socorro is the largest (110 km^2) and highest (1040m) of the four volcanic islands in the Revillagigedo Archipelago (Wehtje et al. 1993) (The archipelago was declared a Biosphere Reserve by the Mexican government in June, 1994). Socorro is probably early Pleistocene in age, based on evidence in the form of erosion shelves (Levin and Moran 1989, Brattstrom 1990). Descriptions of the different habitats on the island, which range from arid coastal scrub to moist montane forest, can be found in Miranda (1960) and Levin and Moran (1989).

We initiated field studies of the surviving population of *Mimodes* in January 1993. One of us (JEMG) subsequently made extended observations on Socorro in 1993 (6 June–5 August) and 1994 (18 February–4 June). Throughout these periods of study we have attempted to color-band and observe *Mimodes* over the entire island. By June, 1994, we had marked 215 Socorro Mockingbirds. We were able to identify the sex of many banded birds from observations of singing birds combined with measurements in the hand. Males average larger in wing and tarsus length (unpubl. data). We could also recognize paired females, regardless of whether they were nesting, because they gave distinctive calls when their mates were vocalizing. After a distant male sang, the females typically gave one or two short, guttural "chunk" calls, and then usually moved towards the vocalizing male. As soon as a female drew close to her mate, she gave a series of more nasal calls we describe as "nya, nya."

We were unable to locate any nests of *Mimodes* in 1993, but we found five in 1994. (We have deposited voucher photographs of nests and eggs with VIREO, accession numbers V06/19/001-003.) All five nests were in forested areas at elevations ranging from 850-950 m, just below the island's summit. All were placed in trees that included *Bumelia socorrensis* (N = 2), *Guettarda insularis* (N = 1), *Ilex socorroensis* (N = 1), and *Meliosma nesites* (N = 1). Dominant canopy trees in the vicinity of all nests were *Guettarda* and *Ilex; Oreopanax xalapense* was common in the subcanopy; and shrubs of *Triumfetta socorrensis* and *Eupatorium pacificum* were also present in the understory near the nests.

All five nests we found were open cups constructed of twigs, similar to those of many other Mimids, and lined with mosses and other epiphytes. Three nests were placed in foliage of outer branches, one in a forked bole of a large tree, and one in a shallow cavity in the side of the trunk of a large tree. The five nests averaged 16 ± 2.6 (SD) cm in outer diameter; the inner diameter was about 8 cm and the cup's depth about 4 cm. The nests were placed 3.7 ± 0.9 m high in trees that averaged 5.4 ± 0.7 m in height.

We observed eggs in three nests: all had bluish-green ground color with large brown spots concentrated at the widest end. The eggs therefore were similar to the eggs of most mockingbirds in the genus *Mimus,* and different from those of most *Toxostoma,* the eggs of which have small brown spots (Bent 1948). We measured three eggs from one nest. These averaged 26.8 ± 0.7 mm in length and 19.5 ± 1.8 mm in width.

The sparse evidence previously available suggested that nesting is concentrated in late winter and early spring. Strong territoriality and birds carrying nesting material had been observed in February (Castellanos and Rodríguez-Estrella 1993), and immatures had been seen in late April and early May (McLellan 1926, Santaella and Sada 1991).

Our observations confirm that many *Mimodes* pairs nest in early spring. Four of the five nests described above were active when discovered by JEMG between 29 March and 20 April 1994. Except for two breeding females, all parents at these nests had received color bands, which helped us to determine the identity of the birds involved in the different nesting activities. By following the banded adults, we found the empty fifth nest on 14 April, in a territory where on 28 March we banded one of two fledglings that may have fledged within the same territory. We also found two nests with three eggs on 7 and 20 April. At these nests, only females were seen incubating. Both nests failed after the females incubated the eggs for at least seven and twelve days respectively; in the latter, the unbanded female disappeared suddenly. The two other nests contained nestlings at the time of discovery. We found one of these on 29 March when the nestling period was fairly advanced; two chicks remained at the nest for at least six days. One chick was color banded on 3 April; on 2 June we saw this bird in a territory 1.6 km from its nest. Of the four nests observed with contents, only this nest is known to have successfully fledged young. The other nest with young contained two recently hatched nestlings and one egg on 11 April. We had seen the banded female from this nest carrying lining material (small, thin pieces of bryophyte) in this vicinity on 23 March; from this, and assuming that eggs are laid in successive days, we estimate an incubation period of no more then 15 days. On 14 April the nest contained three nestlings; the youngsters differed markedly in size. Five days later the youngest chick was absent, and the nest was empty by 23 April. We do not know if these young successfully fledged. If they did, it would indicate a nestling period of 14 days or less.

We also gathered additional evidence that may suggest that the population as a whole has a more extended breeding season. By examining the proportions of banded birds in juvenile, immature, and adult plumage, we conclude that some nesting may take place from November through July. We have found juveniles with spotted breasts from January through July, and immatures with clear breasts and brown irides from February through August. The existence of museum specimens in spotted juvenal plumage in December, January, and

March (K. Parkes, pers. comm.) further supports the possibility of an extended or variable breeding season. In order to reach a clearer understanding of the timing and duration of the complete nesting season, we need to determine the length time needed for the breasts spots characteristic of juvenile Socorro Mockingbirds to disappear.

We watched the foraging activities of the parents at least once for each nest for one hour. Parents perched on branches of *Oreopanax xalapense* and *Meliosma nesites* near their nests while hunting insects. The mockingbirds sat and visually inspected the nearby areas; when a suitable prey was located, the birds left the branch with a powerful flight toward the target. In some occasions the mockingbirds chased the insects flying through branches and bushes in a way that resembled the flight of *Accipiter* hawks. They also searched for insects on the ground. Mockingbirds also foraged in tree canopies when searching for fleshy fruits; they gleaned and probed their beaks on branches with epiphytes. Only putative parents, and no helpers, fed the broods we observed. Parents brought small insects, moths, small butterflies, which were abundant at the time, and caterpillars. We saw no parents carrying whole fruits to the nest in their beaks, but mockingbirds were feeding on the large fruits of *Bumelia* and *Ilex* at the time, and some may have regurgitated fruit pulp to the nestlings. On one occasion, a male arrived at the nest tree and gave a faint call, after which the brooding female left the nest and the male fed the chicks.

Of the four active nests where we found eggs or nestlings, three may have been lost to predators. Red-tailed Hawks (*Buteo jamaicensis soccoroensis*) are likely predators on nestlings and incubating females because some nests were placed near the crown edge. Furthermore, hawks frequently approached us, when we were moving through the vegetation searching for nests, and landed in the tree crowns in a manner that suggested they were hunting. Hawks also approached when mockingbirds we were banding gave distress calls. The endemic *Buteo* is known to prey on shearwaters and Northern Mockingbirds, as well as lizards and lambs (Whetje et al. 1993). Our observations confirm this hawk's potential for preying on nesting birds: on 12 January 1993, we saw a hawk emerge from dense vegetation carrying an adult Townsend's Shearwater. This occurred at high elevation on Socorro's north side, where many shearwater burrows are located (Whetje et al. 1993).

Feral introduced cats probably also prey on mockingbird fledglings, which perch on and near the groud, and are incapable of flight, for several days after leaving the nest. Because adults often forage on the ground, cats may take them as well. Rodríguez-Estrella et al. (1991) argued that predation on birds by cats on Socorro was not very important because only 22.6% of the 31 cat scats they examined had bird remains, including one with remains of *Mimodes* (the authors reported no details about the evidence from this scat). Rodríguez-Estrella et al. (1991) based their conclusion in part on data suggesting that cats were most abundant near the coastal naval base, though they also cited evidence that the distribution of cats was expanding. Our findings suggest that cats currently pose a more serious threat to the island avifauna. We found cat signs at all elevations. We examined stomach contents of 16 trapped cats and found two containing Rufous-sided Towhees (*Pipilo erythrophthalmus socorroensis*), although most remains were of arthropods and of the endemic lizard (*Urosaurus auriculatus*). We also examined 16 cat scats; in 14 (88%) we found bird remains, including Townsend's Shearwaters (*Puffinus auricularis*), Rufous-sided Towhees, Tropical Parulas (*Parula pitiayumi graysoni*), and Socorro Wrens (*Thryomanes sissonii*). We also found several Townsend's Shearwater carcasses on the ground torn apart in a manner that suggests cat predation (cf Veitch 1985); similar evidence of cat predation on shearwaters was found by Jehl and Parkes (1982).

The fact that we found arboreal nests of Socorro Mockingbirds argues against the idea that the decline of this species was caused by cats preying on ground nests, as conjectured—

without any knowledge of the nesting of *Mimodes*—by Jehl and Parkes (1983), or by trampling of nests by sheep. Predation by cats is more likely to occur on fledglings and, possibly, on adults. Nevertheless, it is necessary to determine other potential causes of nest failure, potential nest predators, and predation rates to evaluate the role of predation on the population structure of *Mimodes*. Because we found nests in montane forest areas where sheep impact has been moderate, our observations suggest that the decline of *Mimodes* was caused mainly by habitat destruction: suitable nesting habitat is lacking in highly overgrazed areas, because such habitat no longer provides the relatively unbroken shrubby ground cover and moderately dense trees that Socorro Mockingbirds appear to prefer for nesting. We advocate immediate implementation of a program to eradicate sheep and cat populations on Socorro; these actions may be required in order to avert the extinction of *Mimodes* and other native species such as Townsend's Shearwater considered at risk (Collar et al. 1992).

Acknowledgments.—The senior author dedicates this paper to the memory of his father, Juan Ricardo. We thank the Mexican Navy for generous logistical assistance and hospitality, A. Flores and M. Ramos for their field assistance, and K. C. Parkes, R. Rodríguez, and an anonymous reviewer for their helpful comments on the manuscript. Financial support was provided by the Frank M. Chapman Memorial Fund, the American Ornithologists' Union, the Dept. of Biology at Villanova Univ., and Sigma Xi-the Scientific Research Society.

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Wilson Bull., 107(3), 1995, pp. 555–557

Exceptional response by female Red Crossbills to dietary carotenoid supplementation.—Carotenoid-based pigmentation accounts for much of the yellow, orange, and red coloration of feathers (Brush 1978, Goodwin 1984). It has long been known that animals cannot synthesize carotenoid pigments *de novo* and must obtain such pigments from their diet (Giersberg and Stadie 1933, Brockmann and Völker 1935, Brush 1978, Goodwin 1984). However, the extent to which dietary access to carotenoid pigments can affect individual expression of plumage coloration and can generate variation in color expression within a populations has only recently been emphasized (Brush and Power 1976, Hill 1992, 1993a,b). While the brightness or hue of carotenoid-based plumage can be altered by diet, the distribution of pigmentation across the surface of a bird (i.e., the pattern of coloration) is not generally affected by diet (Hill 1993a). Similarly, in the few species that have been studied, differences between the sexes in expression of carotenoid-based integumentary coloration are not affected by dietary access to carotenoid pigments (Miskimen 1980, Burley et al. 1992, Hill 1993b). Here we report a dramatic change in the plumage coloration of female Red Crossbills (*Loxia curvirostra*) that were fed a diet rich in canthaxanthin during molt.

The Red Crossbill is a sexually dichromatic cardueline finch. Adult males have carotenoid-based ornamental coloration (Völker 1957) over their entire body plumage that varies in appearance from drab yellow to bright red (Tordoff 1952, Jollie 1953, Kemper 1959, Phillips 1977). Most males in definitive plumage are reddish-orange in coloration (Kemper 1959). Females are dull olive-gray to yellow-gray with faint streaking on their flanks and breast that is lacking in adult males (Jollie 1953, Phillips 1977). A few females show a wash of red coloration (Jollie 1953, Phillips 1977). In the wild, however, there is no overlap in the coloration of males and females: the most drably plumaged male is brighter and redder than the most brightly plumaged female (Tordoff 1952, Jollie 1953, Kemper 1959, Phillips 1977).

We used diet supplementation to test the effect on plumage coloration in male and female Red Crossbills. Diets were enhanced with red carotenoid pigments during pre-basic molt. Six male and three female Red Crossbills of call type 5 (Groth 1993) were captured 18-19 September 1993 near Aspen, Colorado, and four male and three female Red Crossbills of call type 2 (Groth 1993) were captured near Los Alamos, New Mexico 5-6 October 1993. Female crossbills of call type 5 were sexed by presence of a brood patch at the time of capture. Females of call type 2 were sexed by plumage. The birds were divided by call type and housed on the campus of New Mexico State University, Las Cruces, in an indoor room that was divided with 1.2 cm mesh screen into two 1.55 × 2.74 × 2.24 m aviaries. Birds were provided with grit and with water containing vitamins and calcium supplement. Fresh cones, usually ponderosa pine (*Pinus ponderosa* var. *scopulorum*), were provided daily, supplemented with sunflower seeds. Fresh pine branches were provided weekly. The red carotenoid pigment canthaxanthin was added to the drinking water of birds in the form of

starch-gel beadlets (Roxathin Red 10 WS, Hoffmann-LaRoche Inc., Nutley, NJ; approximately 0.004 g/ml water). This form of canthaxanthin is stabilized and water soluble.

At the time of capture most males of both call types were drab red-orange over their entire body plumage, and females were olive-gray. A few males were drab orange with patches of yellow plumage. All individuals underwent complete pre-basic molt in captivity from November 1993 to January 1994. At the completion of molt, the body plumage of both males and females was bright red-orange, and the sexes were indistinguishable. All males showed brighter plumage after captive molt than at the time of capture, and all females showed much brighter plumage after captive molt, having changed from drab olive-gray to bright orangish-red. There was no difference between birds from the two call types.

To our knowledge, this is the first example of sex-specific plumage coloration being completely obscured by response to dietary pigment supplementation. The effects of carotenoid supplementation on the expression of plumage coloration in female House Finches (*Carpodacus mexicanus*) were quite different. The House Finch is a sexually dichromatic cardueline finch with carotenoid-based plumage coloration that is similar to that of Red Crossbills (Brush and Power 1976, Hill 1992, 1993a). Feeding female House Finches large quantities of canthaxanthin during molt caused them to grow redder and more extensively pigmented plumage than they had displayed at the time of capture (Hill 1993b), but sex-specific differences in plumage pigmentation were not obscured. The brightest female House Finch from the feeding experiment was still less intensely pigmented than the drabbest male (either captive or wild), and females from the feeding experiment retained their sex-specific plumage pattern with heavy melanin streaking on the throat and upper breast, fore crown, and rump (Hill 1993b). Moreover, carotenoid supplementation in the House Finch did not cause females to express plumage pigmentation beyond that seen in wild populations; the most brightly plumaged female from the feeding experiment showed plumage pigmentation very similar to that of the most brightly pigmented females in wild populations (Hill 1993b).

Compared to House Finches, Red Crossbills differ much less between the sexes in melanin pigmentation (females show faint ventral streaking that is lacking in males). Sex-specific plumage differences are primarily differences in plumage hue and brightness, not in the distribution of feathers with carotenoid pigmentation. Therefore, to change from a female-typical to a male-typical appearance in the Red Crossbill, all that is required is to brighten and redden the plumage. We found that such change was effected by carotenoid supplementation.

A small proportion of wild female Red Crossbills from all geographic races show some red coloration in their plumage (Jollie 1953, Phillips 1977). We know of no reports, however, of wild female Red Crossbills displaying male-like plumage. If all female Red Crossbills have the potential to grow bright red plumage, and yet such coloration is not seen in wild females, this suggests that wild females do not obtain sufficient dietary carotenoids for full expression of plumage coloration. Because most male Red Crossbills have bright red plumage, one might surmise that they consume substantially more carotenoid pigments than females during molt. This assumes, however, that male and female Red Crossbills have the same physiological mechanisms for carotenoid uptake, transport, and deposition (Brush 1990). More likely, there are substantial sex-specific differences in such physiological mechanisms that may or may not be compounded by sex-specific differences in dietary intake of carotenoid pigments. Only in situations where birds consume huge quantities of carotenoid pigments, such as feeding experiments, are differences in physiology between the sexes overwhelmed. Nevertheless, revealing the capacity for male-like color expression in females of a highly dichromatic bird is interesting and further indicates that much remains to be learned about the proximate control of plumage coloration.

Acknowledgments.—Field and aviary work was supported by research funds from the

Dept. of Biology, New Mexico State Univ., to CWB. Mary Joan Gwyther and the Hoffman-LaRoche Chemical Company kindly donated the carotenoids used in feeding experiments.

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Wilson Bull., 107(3), 1995, pp. 558–561

Winter food of a small insectivorous bird, the Golden-crowned Kinglet.—Kinglets are the smallest passerine birds in the world, averaging 5–6 g. Since small body mass poses high energetic demands on thermoregulation, kinglets should face stringent problems of maintaining energy balance (Walsberg 1983). How they maintain energy balance in northern environments where temperatures routinely dip to −30°C and less, while on an insectivorous diet is not known. However, kinglets help reduce the extreme metabolic crunch imposed by their small size by huddling at night (Thaler 1990) or by at least sometimes sleeping in sheltered locations such as insulated squirrel (Blem and Pagels 1984) or bird nests (Farley 1993).

Most insectivorous birds of the northern forests solve the energy problem by migrating when insects become scarce at the end of the summer. Exceptions include birds that can access insects hidden inside wood (woodpeckers), or in bark crevices (parids, creepers, and nuthatches), and/or that can turn to alternative foods (suet and seeds) when available. Kinglets are unable to access insects hidden from view (Thaler 1990), and they never visit human-provided food in winter.

In the summer the Golden-crowned Kinglet (*Regulus satrapa*) subsists on a great variety of insects (Crawford and Jennings 1989, Galati 1991). However, their diet in the winter was previously unknown. The European winter kinglet the Goldcrest (*R. regulus*), is thought on the basis of its foraging mode to be a Collembolan specialist (Harrison 1969), and its main winter food is thought to be collembolans, genus *Entomobrya* (Schmidt 1968, Thaler 1990).

In the coniferous forests of western Maine, the site of this study, at least some (or all?) of the population of Golden-crowned Kinglets (*R. satrapa*) are year-round residents. The area is characterized by deep winter snows and temperatures that routinely dip to −30°C and sometimes to lower than −40°C (as in the winter of 1993–1994). The birds were present throughout all winters examined, although they seemed to be noticeably less common the winter of 1993–1994. (Curiously, 13 of our sample of 16 birds were males). They occurred in flocks of 2–4 individuals that moved rapidly through spruce-fir forests from dawn till dusk. Do they subsist on "snow fleas," the collembolan *Hypogastrura nivicola* (Hypogastruridae) that appear by the millions even on the deepest snow within hours of every thaw in the winter?

We examined the gizzard contents of 15 Golden-crowned Kinglets, all foraging in spruce-fir stands, from late November to mid-April, and one from mid-May, 1992–1994. Since our diet analysis is based on the hard exoskeletal remains, it may underestimate the contribution of soft-bodied prey. However, since the gizzard contents of the foraging birds were suspended in isopropyl alcohol within 1–2 min of collection (by 22 caliber rifle), digestion should have been stopped, and remains of the most recently ingested insects should have remained. Our emphasis, however, was in determining the *kinds* of prey. Thus, presence of prey was based on as little as a leg or a mandible fragment (spider) or several scales (moth), to almost wholly preserved specimens (two collembolans, many caterpillars). Unless two parts clearly came from two individuals (i.e., two right wings) we conservatively assigned them to one.

We made a "spot check" of prey availability by spreading a $5m^2$ white sheet under small (8–15 cm diameter) trees or tree branches of similar size and hitting them twice each as hard as possible with the blunt side of an ax. On 13 October 1991 (following leaf fall and nightly frosts), a survey of five white pine (*Pinus strobus*), five red spruce (*Picea rubra*) vs five deciduous trees/branches (principally maple [*Acer*] and birch [*Betula*]) yielded 80, 122, and 11 arthropods, respectively. They were 119 spiders, 53 homopteran, 18 diptera, 13

TABLE 1

FOOD ITEMS IDENTIFIED IN THE GIZZARDS OF 16 GOLDEN-CROWNED KINGLETS

	Kinglets																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
Seeds	0	0	0	0	0	0	0	0	0	0	0	0	10	3	17	3	33
RFM	0	0	+	0	+	+	0	0	0	0	0	0	0	0	0	0	—
Diptera																	
Adult	0	0	0	1B 1Ce	0	0	0	0	0	2	0	0	0	1	0	0	7
Pupae	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
Larvae	24A	1S+ 6T	1S+ 13T	2S+ 8T	1S+ 14T	2S+ 17T	0	1T	0	1	0	1T	0	0	0	0	93
Homoptera	0	0	0	0	1P	1Ap	1Ap 1Ci	0	0	0	0	0	0	0	0	2Ap	6
Plecoptera	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Heteroptera	0	0	0	0	0	0	>1N	0	0	0	0	0	0	0	0	0	1
Neuroptera	0	0	0	0	0	0	1H	0	0	0	0	0	0	0	0	0	1
Hymenoptera	0	1Br	0	0	0	0	1	0	0	1	0	0	0	0	0	0	3
Lepidoptera																	
Pupae	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3
Larvae	30G	16G	1G 12oth.	29G	38G 1oth.	10G	6G	19G	8G	2G	26G	17G	6G	23G 1oth.	6G	35G 1oth.	272G 15oth.
Adults	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arthropod eggs	0	3	3	0	0	7	0	0	1	0	0	0	2	0	3		21
Arachnida	1Sp	1Sp	1Sp	1Sp	1Sp	0	1Sp 1Mi	1	0	0	0	1	0	0	0	2 0	9
Coleoptera	0	0	0	0	0	0	3E 1M	0	1C	0	0	2Ca	0	0	1	0	8
Collembola	4(2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4

[a] The top row identifies the 16 kinglets. Dates of capture were as follows: 1, Jan. 25, 1992; 2–4, Dec. 1992; 3–7, March–May 11, 1993; 8–12, April 14, 1994; 13–16, Nov. 24–26, 1994. Numbers in body of table show minimum number of prey items of indicated category. Letters refer to type of prey items: A = Agromyzidae (Diptera) larvae, Ap = Aphidae (Homoptera), B = Bibio sp. (Bibimidae, Diptera) adult, Br = Braconidae (Hymenoptera) adult, C = Curculionidae (Coleoptera) adult, Ca = Cantharidae (Coleoptera) larvae, Ce = Cecidomyidae, Lestreminae (Diptera) adult, Ci = Cicadellidae (Homoptera), E = Elateridae (Coleoptera) adult, Geo = Geometridae (Lepidoptera) larvae, H = Hemerobiidae (Neuroptera) larvae, M = *Mulsantina hudsonica* (Csy.) (Coccinellidae, Coleoptera) adult, Mi = mites (Arachnida), N = *Nabis americoferus* Caragon (Heteroptera) adults, oth. = larvae other than Geometridae (Lepidoptera), P = *Paratrioza* sp. (Psyllidae, Homoptera) adult, Pu = pupae (Lepidoptera), RFM = unidentified red flocculant material, S = Syrphidae (Diptera) larvae, Sp = spiders (Arachnida), T = Tachinidae (Diptera) larvae parasitizing lepidopteran caterpillars.

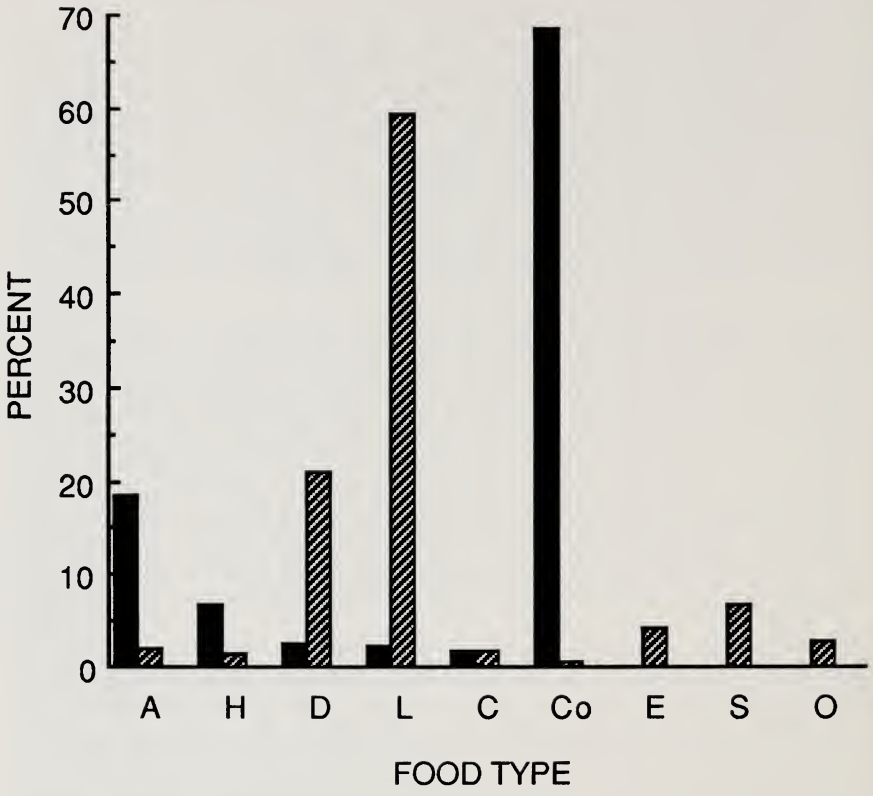

FIG. 1. The relative percentage of the most common types of arthropods (N = 795) retrieved from winter tree branches (filled bars) vs the most common types of prey items (N = 483) found in the kinglets' stomachs (hatched bars). A = Arachnida, H = Homoptera, D = Diptera, C = Coleoptera, L = Lepidoptera (caterpillars), Co = Collembola, E = Arthropod eggs, S = seeds, O = other.

coleoptera, and 13 caterpillars. On 1 December, 1991, 10 conifer branches yielded 532 collembolans (*Hypogastrura nivicola*), 27 spiders, two geometrids, one homopteran, and one fly, while 10 red (*Acer rubrum*) and sugar maple (*A. saccharum*) trees/branches yielded only 13, one, two, zero and zero of the same arthropods, respectively. An additional sampling occurred on 10 January, 1995, during a thaw following several days when temperatures had dipped to at least −30°C. Fifteen each of 5–8cm diameter red spruce, balsam fir (*Abies balsamea*), red maple and American beech (*Fagus grandifolia*) were sampled as before (on snow). The total arthropods taken was 25 spiders, 13 geometrid caterpillars, one beetle, one fly, and >50 *H. nivicola.* Three of the caterpillars were on the balsam fir, the other ten were on the maple and beech. Thus collembolans were present on winter conifer branches, which also consistently had many more arthropods than deciduous branches of similar thickness. By far (>99%) the most numerous collembolan were the "snow fleas," *Hypogastrura nivicola* (Hypogastruridae). They peppered the deep snow by the millions within hours of every

thaw, and then retreated primarily into the bark crevices of thick trees during the intervening cold periods. However, in contrast to our expectations that these insects would be the kinglet's primary food, given previously-published accounts of the foraging specializations of kinglets, our study pointed to a different conclusion.

Out of a total of 483 identified prey items in the gizzards of the 16 Golden-crowned Kinglets in winter, 287 (or 59%) were lepidopterous caterpillars (of which 60 were parasitized by Tachinid fly larvae), and of all these caterpillars, 95% were geometrids (Table 1). Small (5–10 mm) lepidopterous larvae were the only consistent diet items found in all 16 birds, with a mean of 18 per bird (range = 6–39). Additionally, remains of numerous other (Table 1) kinds of arthropod food items were retrieved, but all appeared only sporadically among the different individuals. Four individuals had eaten small seeds, and three had red flocculant (presumably fruit) in their gizzards. In the 11 birds from late November to April, any one bird had recently fed on 3–7 kinds of food items, while the one bird from mid-May had fed on ten. Noticeably absent in the diet, despite their abundance in the environment, were collembolans. Only one of the 16 birds had collembolans, and the four it had eaten were of at least two species, neither one being *H. nivicola,* the hyperabundant "snow flea." We were surprised that so many caterpillars were apparently hibernating in the open treetops in the depth of winter.

We conclude that the kinglets' foraging in evergreens may reflect prey abundance there, but that they do not prey on the there very abundant *H. nivicola.* The diet of the kinglets appears to be varied and highly opportunistic. Furthermore, although the birds include some species of *Collembola* in their winter diet, they appear to subsist primarily on geometrid caterpillars. Our estimate of primary reliance on lepidopterous caterpillars (Fig. 1) is a conservative one because we tabulated only numbers of items, and the volume of individual caterpillars was far greater than the volume of most of the other prey items such as aphids, arthropod eggs, seeds, etc. that we tabulated. This study was done under State of Maine Collecting Permit No. 75-1743.

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Wilson Bull., 107(3), 1995, pp. 562–563

First nesting record of the Great-tailed Grackle in Oregon.—We report here the first published record of the Great-tailed Grackle (*Quiscalus mexicanus*) breeding in Oregon. During the third week of May 1994, a pair of Great-tailed Grackles was observed at the headquarters of Malheur National Wildlife Refuge, ca 55 km SSE of Burns, Harney Co., Oregon. They remained in the area for several months through the summer. The male was the most visible, often seen calling and singing from the tops of a small stand of Russian olives (*Eleagnus angustifolia*) surrounding a spring-fed pond. On 7 July, the female was observed carrying food into a Russian olive tree. Both the male and female frequently were observed the following week, often picking dead insects from parked vehicles around the headquarters area. On 13 July, their nest was located by the authors in one of the Russian olive trees. The male was present and performed distraction displays. The nest was ca 3 m above the ground and 4.8 m from water. It consisted of an outer structure attached to the tree at three spots which supported a smaller bowl inside. The outer structure of the nest consisted of Hardstem bulrush *(Scirpus acutus)* and the inner bowl was made up of sedges (*Carex* spp.) and grasses. The nest measured 14 cm from the top of the outer structure to the bottom and 15 cm wide across the outer structure and inner bowl. On 15 July, one nestling was found in the nest and both male and female were present performing distractive displays. On 29 July, the nest bowl was empty and the nestling had fledged. The family group remained at the headquarters area through late October.

The Great-tailed Grackle was first recorded in Oregon on 16 May 1980, when an adult male was observed at Malheur Field Station, ca 50 km SSE of Burns, Harney County, Oregon (Littlefield 1983). Several more records for Harney County were added in 1980 and 1981, but no additional individuals were recorded in the area until one was seen at Malheur Field Station on 9 May 1985 (Littlefield 1990). Additional Great-tailed Grackles were seen in the area in the springs of 1986, 1987, 1989, 1990, 1993, and 1994 and in the fall of 1990. Outside of southeast Oregon, two were present in northeast Oregon at John Day Fossil Beds National Monument, Grant Co., on 18 May 1980 (Littlefield 1983), and another reached northeast Oregon near La Grande, Union Co., on 5 June 1980 (Rogers 1980). An individual was recorded near Madras, Jefferson Co., on 23 May 1992 (Evanich 1992), for the westernmost state record and two were recorded at Umatilla National Wildlife Refuge, Morrow, Co., on 24 May 1993 (Summers 1993), for the northernmost record in the state.

All recorded individuals were adult males, and only two records of females previously have been noted. On 14 October 1989, a single female was observed at Fields, Harney Co. (Anderson 1990), and a second record for a female was obtained at Fields on 27 September 1993 (Summers 1994). No female Great-tailed Grackles had been detected in the spring before 1994 when a female was found with a male at Malheur National Wildlife Refuge headquarters. Furthermore, no nesting records for this species have been documented in Oregon in the past. During the past ten years it appears that nesting by Great-tailed Grackles increased in the area extending from southern Nevada northward to southeast Oregon (Holmes et al. 1985).

The first nesting record for Nevada was obtained in 1980. A single active nest was found at Beatty, Nye Co., in the southern portion of the state (Kingery 1980). A second nesting record for Nevada came during the summer of 1983 in Carvers, Nye Co. (Holmes et al. 1985). Adult male and female grackles were again observed at the same location between 22 May and 15 July 1984, although it was not determined whether they nested there. Northern California obtained its first record of nesting Great-tailed Grackles in June 1980 when a pair attempted to nest in San Francisco (Laymon and Shuford 1980). In Utah, Great-tailed Grackles first appeared in 1979, and in 1985 five nesting sites were located in the southwest

segment of the state (Kingery and Lawson 1985). In 1986 a pair reached northwest Utah and began nesting at Tooele, Tooele Co. (Kingery 1986). No nesting records of Great-tailed Grackles have yet to be confirmed in Idaho, however males and females were observed exhibiting courtship behavior during the 1994 breeding season in the Twin Falls and Burley areas, Twin Falls and Cassia Cos., and nesting is thought to have occurred. (C. Trost, pers. comm.).

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Wilson Bull., 107(3), 1995, pp. 563–565

Ground-nesting Long-eared Owls.—The Long-eared Owl (*Asio otus*) is widely distributed throughout the northern hemisphere (Cramp 1985). It generally occurs in temperate northern latitudes and nests primarily in old stick nests in trees or shrubs built by hawks, corvids, and squirrels (Cramp 1985). However, a few nests have been reported on the ground in Britain (Glue 1977; N = 10), Finland (v. Haartman et. al., in Mikkola 1983; N = 2), Netherlands (Wijnandts 1984; N = 1), and Canada (Bent 1938; N = 1, Campbell et al. 1990; N = 1). Herein, we report the first record of ground-nesting by this species in the United States and one from western Canada. We also provide detailed data on the U.S. nest, data on the Canadian nest, and previously unreported data on a nest reported in Campbell et al. (1990).

Since 1986, DWH has conducted a year-round study of Long-eared Owls in west-central

Montana. Over 600 owls have been banded during the breeding and non-breeding seasons. On 24 May 1994, MTM and DWH flushed a female Long-eared Owl from a ground nest that contained five eggs. The owl flew approximately 20 m and perched high in a tree. This is typical of females flushed off the nest. We then immediately left the area.

On 25 May 1994 we returned, captured, and banded the female and measured the nest dimensions. A distinct nest bowl was evident and measured 16 cm in diameter and 4 cm deep. The cup did not appear to be passively formed by an incubating bird. It consisted of an earthen surface, with the vegetation removed, surrounded by a ring of cut grass. The nest was in a planted shelterbelt, approximately 2 km long and 35 m wide. It was under a rose bush (*Rosa woodsii*) at the base of a Siberian elm (*Ulmus pumila*) and surrounded by tall grasses. The closest unoccupied stick nest was 38 m south and had been used in past years by Long-eared Owls. A second stick nest, 100 m to the north was occupied by Long-eared Owls early in the season but was abandoned approximately three weeks before the ground nest was discovered. A third stick nest previously used by Long-eared Owls was 195 m south. Two other intact stick nests were within a 200 m radius of the nest. To our knowledge, they had not been used by Long-eared Owls in the past.

On 24 June 1994, we captured the male Long-eared Owl defending the nesting female and young. He had been banded as a nestling in 1993 in a stick nest 3.5 m above the ground in a tree and approximately 200 m south of the ground nest. We banded all five nestlings on this visit (two to three weeks of age).

Between 30 June and 6 July 1994, all five nestlings had dispersed from the nest and "branched" to nearby trees. The female also left the area during this period also. The young were three to four weeks old. On 9 August, all five young were captured and capable of sustained flight. The male was not located. On 26 August, no Long-eared Owls were in the area. The scenario was similar to other Long-eared Owls nesting in tree stick nests in the study area (authors' observation).

A ground-nesting Long-eared Owl was located by RWC on 22 April 1990 north of Oliver in the southern Okanagan Valley, British Columbia, Canada. The nest was on a slightly raised hummock under rose bushes (*Rosa* spp.). The immediate area was surrounded by water, the nest site being dry. Surrounding trees were mainly trembling aspen (*Populus tremuloides*) and tall willows (*Salix* spp.) in a semi-open area. An incubating adult was flushed from the nest which contained five eggs. Five nestlings were seen in the nest on 7 and 15 May. Four nestlings were seen on 20 May. On 31 May, three "branchers" were seen in the immediate area, suggesting success. No other observations were made.

On 22 June 1961, James Grant (corres. to RWC) discovered a ground-nesting Long-eared Owl 17.7 km north of Vernon, Okanagan Valley, British Columbia, Canada (see Campbell et. al. 1990). The nest was beside a pile of ponderosa pine (*Pinus ponderosa*) branches in an opening of dense pole-sized Douglas-fir (*Pseudotsuga menziesii*) trees. The area had been logged 15–20 years previously. The nest was sheltered by 1-m high snowberries (*Symphocarpus albus*) as well as roses. The female was on the nest with five nestlings. The nestlings fledged by 16 July.

Typically, Snowy Owls (*Nyctea scandiaca*) and Short-eared Owls (*Asio flammeus*) are the only true ground-nesting owls of North America, while the Burrowing Owl (*Speotyto cunicularia*) nests underground. A few accounts of ground-nesting by other North American owls have been reported: Great Horned Owls (*Bubo virginianus*) (Bent 1938), Barn Owls (*Tyto alba*) (Tewes 1984), Great Gray Owls (*Strix nebulosa*) (Bull and Duncan 1993), and Barred Owls (*Strix varia*) (Robertson 1959). But, a literature search indicates that ground-nesting Long-eared Owls are very unusual. In five North American Long-eared Owl studies, only two in 317 nests (0.6%) were found on the ground (Bull et. al. 1989; N = 20, Campbell 1990; N = 61, Holt, unpublished data; N = 67, Marks 1986; N = 112, Peck and James, in

Johnsgard 1988; N = 57). In Europe, it appears to be better documented, but still unusual. Of 570 Long-eared Owl nests documented in Britain, Finland, and Netherlands, only 1.9% (N = 11) were found on the ground (Glue 1977; N = 256, Mikkola 1983; N = 101, Wijnandts 1984; N = 213).

In past cases of ground-nesting Long-eared Owls, Bent (1938) and Glue (1977) both suggest that ground-nesting was due to a scarcity of suitable tree nests or suitable platforms. We do not believe the ground nest in western Montana can be explained by a scarcity of suitable sites, since five vacant stick nests occurred within 200 m of the ground-nest. And, three nests had been used by Long-eared Owls in the past.

Acknowledgments.—We thank Jeff Marks and Rick Amon for comments.

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Wilson Bull., 107(3), 1995, pp. 565–567

Gray Flycatcher predation on a hummingbird.—On 28 July 1991 at 08:08 EST at the Archbold Tropical Research Center, Springfield Field Station (15°21′N, 61°23′W), Dominica, West Indies, we saw a Gray Flycatcher (*Tyrannus dominicensis*) flying over a lawn with

a large food item in its bill. The habitat around the center is deciduous forest, mature second-growth, and cultivated plots. The flycatcher perched on an electrical wire approximately 20 m from the observers and 6 m above the ground. The prey was identified as a live hummingbird of the genus *Eulampis,* but its specific identity could not be established at that time or later. Two similar species occur at that site, the Purple-throated Carib (*E. jugularis*) and the Green-throated Carib (*E. holosericeus*) (pers. obs.; Chavez-Ramirez and Dowd 1992).

The flycatcher held the hummingbird sideways across its bill and killed it by beating the prey's head and neck against the wire. This technique, which involves vigorous lateral downward movements of the predator's head, has been described for Gray Flycatchers killing large insects (Wetmore 1916; pers. obs.) and small fishes (Lefebvre and Spahn 1987). The hummingbird probably died from the first few strokes; thereafter, it was inert and its neck was loose. The flycatcher then tossed the hummingbird a few cm up in the air, caught it in its bill so that the hummingbird's head was now hanging on the other side of the flycatcher's head, and hammered it again on the wire. This maneuver was repeated two or three times; on each occasion, the flycatcher struck the hummingbird's head two to five times against the wire. The flycatcher then tossed its prey up in the air and tried to catch it by the head, most probably to be able to swallow it head first. On the second such attempt, the flycatcher dropped the hummingbird which fell into 2 m high grass. The flycatcher almost immediately left. We were unable to find the corpse. The total observation lasted less than 2 min.

Apart from cases involving raptors (Falconiformes and Strigiformes) and shrikes (Laniidae), there are very few reports of birds preying on healthy adult birds. Chuck-will's-widows (*Caprimulgus carolinensis*)catch and swallow small birds (Terres 1982). Davidson (1994) reported that within a period of 22 days a single Common Grackle (*Quiscalus quiscula*) killed and consumed at least 39 small passerines of four species. Wright (1962) observed a Northern Oriole (*Icterus galbula*) killing a Ruby-throated Hummingbird (*Archilochus colubris*) at a flowering tree, but the hummingbird was dropped before it could be consumed. There are three reports of Brown-crested Flycatchers (*Myiarchus tyrannulus*) successfully preying on hummingbirds (Snider 1971a, b; Gamboa 1977). Our report provides another case of a tyrannid preying on a hummingbird.

Hummingbirds seem to be the most frequent avian prey of non-raptorial birds, but they rarely are consumed by raptors. There are three reports of Merlins (*Falco columbarius*) preying on hummingbirds (Sprot 1927, Lowery 1938, Mayr 1966) and one observation of a Sharp-shinned Hawk (*Accipiter striatus*) catching an Anna's Hummingbird (*Calypte anna*; Peeters 1963). A hummingbird bill was also found in the nest of a Puerto Rican Sharp-shinned Hawk (Apanius, unpubl. obs.). The small size of hummingbirds probably makes them unattractive for most true predators while, on the other hand, this same characteristic and their slow speed when hovering makes then vulnerable to opportunistic predation by large insectivorous birds.

The Gray Flycatcher feeds mainly on large insects taken on the wing or captured in foliage or on the ground (Bent 1942). The species also regularly eats berries and, more rarely, *Anolis* lizards (e.g., Wunderle 1981), fishes (Lefebvre and Spahn 1987), and hummingbirds (this report). These observations support the suggestion of Wunderle (1981) that certain insectivorous birds may broaden their diet opportunistically by catching novel prey using hunting techniques normally used to capture large insects. However, there was no indication in the case reported here that predation on an alternative prey was the consequence of a scarcity of insects, as was hypothesized for hummingbirds caught by Brown-crested Flycatchers in Arizona (Snider 1971a, b).

Acknowledgments.—G. Seutin was supported by a postdoctoral fellowship from the Nat-

ural Sciences and Engineering Research Council (NSERC) of Canada. Field Work was funded by a grant from the National Geographic Society to Robert E. Ricklefs. We are grateful to William A. Schew and Doug Wechsler for their help in the field, and to the personnel of the Springfield Field Station for logistical support.

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Wilson Bull., 107(3), 1995, pp. 568–574

ORNITHOLOGICAL LITERATURE

Edited by William E. Davis, Jr.

Blackburn's Birds: the Bird Paintings of Jemima Blackburn. Rob Fairley, ed. Canongate Press, Edinburgh, Scotland. 1993: 112 pp., 100 color paintings, 3 black-and-white drawings, portrait photograph. $50.00 (cloth). Distributed in the United States by Trafalgar Square, North Pomfret, Vermont.—This large-format book (9⅝ × 11¼ in.) deservedly brings to our attention the work of an all-but-forgotten Scottish artist and amateur ornithologist, Jemima Blackburn (1823–1909). She wrote and illustrated a number of books, several intended for children. Her ornithological *magnum opus* was the second edition of her "Birds from Nature" (1868). Although she was an admirer of the great folio monographs of Audubon, Gould, and others of the mid-Nineteenth Century, she realized that these were luxury items that only the very rich could afford. She therefore decided to have her illustrations reproduced in black and white, and the first edition (1862) of her book was sold for a modest ten shillings sixpence. As a perfectionist, Mrs. Blackburn was dissatisfied with the book, and in 1868 published an enlarged edition with 22 additional plates. Only six copies were colored by hand for sale to the general public, and another colored copy was produced for a friend's birthday.

The editor of the present book, Scottish artist Rob Fairley, was chatting one day around 1983 with Alan Blackburn, a friend and neighbor of some years, when Blackburn casually mentioned that his great-grandmother Jemima was a painter. Fairley paid little attention until Blackburn persuaded him to have a look at the paintings, stored in his mother's house. Struck by the beauty and accuracy of the bird paintings, Fairley became determined to revive interest in Jemima Blackburn's life and work, and this book is the result.

Most of the book's illustrations were taken directly from Mrs. Blackburn's originals rather than from published versions; in fact, many, perhaps the majority, have not been previously reproduced. Most are watercolors, with early paintings often including some ink work. A few are collages, in which she cut out a bird's outline and transfered it to a different background, much as was also done by Audubon.

Fairley mentions that some of the paintings, such as that of the Nightjar (*Caprimulgus europaeus*), were done on brown paper; in that painting and the domestic pigeon (*Columba livia*) on the facing page, it is obvious that white areas were painted onto the brown background. But in the majority of the plates in this book, the backgrounds *and* the areas of the birds that should be white are a disconcerting yellowish or buffy color; this may possibly be a literal reproduction of the discoloration of originally white paper.

As evidenced both by the extracts from Mrs. Blackburn's writings (which constitute the bulk of the text of the book) and the paintings themselves, many of her subjects were painted directly from living birds, either pets, as with the Common Raven (*Corvus corax*), or birds held temporarily in captivity. She was particularly successful with young birds, such as the downy chicks of the Common Sandpiper (*Actitis hypoleucos*) and Common Tern (*Sterna hirundo*). A few of the adult birds, such as the Reed Bunting (*Emberiza schoeniclus*) and Yellowhammer (*E. citrinella*), resemble the stiff paintings done from poorly mounted birds typical of much of the older school of bird art. There is an Audubonian liveliness to her painting of crossbills, which, incidentally, are the distinctively large-billed Scottish Crossbills (*Loxia scotica*) which had not been recognized as a separate species in Mrs. Blackwell's day. It would have been useful to have had dates attached to the paintings to verify what one can deduce was her increasing skill in painting lifelike birds. Some, such as the Eurasian

Wigeon (*Anas penelope*) and the Tufted Duck (*Aythya fuligula*) are downright bad, but the head portraits of the Common Raven and the Gray Heron (*Ardea cinerea*) could pass for studies by Fuertes, than which there is no greater praise.

There is one misidentification; the left-hand painting on p. 48 is identified as being that of the Stonechat (*Saxicola torquata*), but the reproductions are clearly two slightly different variants of a painting of Whinchats (*S. rubetra*).

Mrs. Blackburn was a keen observer of bird behavior, as amply evidenced by the excerpts from her writings included in the book. Most striking of all is her detailed account of the ejection of nestling Meadow Pipits (*Anthus pratensis*) by a blind and naked hatchling Common Cuckoo (*Cuculus canorus*), accompanied by a small but dramatic drawing. This behavior had been reported by Jenner in 1788 but dismissed as impossible by Waterton in 1836. Mrs. Blackburn's account was originally published, not in a scientific journal, but in what Fairley calls "a popular but rather poor narrative for children, *The Pipits* (1871)". Darwin refers to Mrs. Blackburn's observations in the sixth edition of "The Origin of Species."

Rob Fairley has done the history of ornithology in general, and of bird painting in particular, a fine service by bringing to our attention the life and work of Jemima Blackburn, who had a distinct influence on her younger but much better known contemporary, Beatrix Potter.—Kenneth C. Parkes.

Ecology and Management of the Wood Duck. By Frank C. Bellrose and Daniel J. Holm. Stackpole Books, Mechanicsburg, Pennsylvania. 1994:588 pp., numerous black-and-white sketches and black-and-white photographs, 8 color-coded maps, glossaries of biological and statistical terms, 226 tables, 131 figures, 11 appendices, 28-pages of references, index. $59.95.—This, the most comprehensive treatment of the Wood Duck (*Aix sponsa*) to date, begins with an introduction that treats the role of Wood Ducks in prehistoric cultures, their appearance on U.S. Postage stamps and on federal and state duck stamps, and the accounts and art of early North American explorers and naturalists. The 19 chapters that follow focus on everything from distribution and habitats to behavior, physiology, parasites, diseases, and management. Tables, figures, and appendices contain an incredible wealth of both new and previously published data about virtually all aspects of Wood Duck biology. These data are generally woven together with a text that is a good review of the literature, fleshed out with original data and analyses. Most aspects of behavior and ecology are illustrated with exceptionally good black-and-white photographs. In short, the authors have done everything but squeeze the "*Aix*!" out of Wood Ducks.

To this endorsement, I must add that it is sometimes difficult to interpret the data for lack of sample sizes and explanation of how data were collected. One could go to the original source for data from previous publications, but that isn't an option in the case of data presented for the first time. For example, tables 78, 79, and 80 present apparently new data on percentage of time spent at various activities by Wood Ducks in Illinois. *P*-values are presented, indicating results of paired *t*-tests, but neither total amount of time spent observing the birds nor the number of birds observed, let alone such factors as habitat or weather conditions, are given. The authors also present interesting data on variation in European Starling (*Sturnus vulgaris*) use of nest boxes supplied with a sawdust nest substrate of different colors (p. 284). Again *P*-values suggest significant differences (Starlings seemed to prefer lighter substrate), but no sample sizes or other details are presented. I hope the details of these studies are yet to come in journal articles.

There are some inconsistencies in presentation. For example, text descriptions of winter distribution of Wood Ducks describe numbers and patterns based in part on Audubon Christmas Bird Counts for the years 1983-87 (why these years and not more?). Map 3, however, shows relative winter densities based on the Audubon Christmas Bird Count for 1979–1980.

The authors clearly demonstrate that this is a very intensively studied species, but for many aspects of the Wood Duck's biology they have been able to provide little synthesis or summary. Tables and figures tend to be study specific, with few data that are compared across studies or regions. Some tables that do summarize data for broad regions are inadequate because of a weak data set. For example, Table 131, which occupies one and one-half pages, presents a tabulation of some vertebrate species that have used Wood Duck nest boxes on national wildlife refuges. Only selected refuges are included, with no mention of why these were selected and others weren't. The "various animals" included in the table are often generic, such as "squirrels," "woodpecker," and "wren." Data are presented for varying numbers of years/refuge (only 1979 for many), there is no indication of the numbers of Wood Duck boxes provided per refuge, the intensity of box checks, who collected the data, or the relative frequency with which species were found using boxes. Having checked a few Wood Duck boxes over the years, I cannot imagine, for example, that Hillside National Wildlife Refuge (NWR) in Mississippi would have had use of boxes by only European Starlings and Northern Flickers (*Colaptes auratus*) and that Eufaula NWR, Alabama, would have use only by Starlings. I question the use of Wood Duck boxes by Tree Swallows (*Tachycineta bicolor*) at Catahoula NWR, Louisiana, since they have rarely nested in the lower mid-South.

The black-and-white photographs add considerable to the book but would have been easier to refer to if they had been numbered. The color-coded maps are useful, but not as useful as they might have been. Map 1, for example, includes four separate maps indicating levels of density as well as the current breeding range for Wood Ducks. Density levels given are "sparse," "low," "medium," and "high," but no source for the information on the maps is given nor are the meanings of the density levels presented. It is difficult to visualize the total range from these—a composite is really needed. The five and one-half page index is useful, but inadequate for a 588-page book. Don't depend on it! For example, under Mississippi, there are three page numbers given, yet I found Mississippi mentioned with important data presented in tables and appendices on dozens of other pages.

Errors in the book tend to be in materials somewhat peripheral to Wood Ducks. For example, the authors refer to the brown rat snake (p. 295), which is not a recognized common name for any North American snake, when they apparently meant to refer to the gray rat snake (*Elaphe obsoleta spiloides*). Also, I question that "Flickers also may make tiny holes in Wood Duck eggshells, apparently in an attempt to cause nest abandonment" (p. 294). A tiny hole is all that is needed for a woodpecker to insert its tongue to feed on the contents.

This is the sort of book that tends to be viewed as a "comprehensive review" up until the year of publication. Is it? A scan of the references suggests that serious review of the literature ended with 1990, and that the most recent citation is from 1992. The authors do not refer to their list of literature as a "Literature Cited" section—it is called "References." A perusal of the references suggests that there is reason for this. While I found no reference cited in the text that was missing from the list of references, I quickly found references in the list that are apparently not cited in the text (for example, Jackson (1974) and Rudolph et al. (1990)). This list of references is of great value: included within it are more than 60 M.S. or M.A. theses and more than 20 Ph.D. dissertations, as well as an abundance of citations to unpublished government reports.

For those interested in duck biology, wetland ecosystems, and Wood Ducks in particular,

this is a "must" publication. The list of references alone should be required reading for any graduate student contemplating study of Wood Ducks. No doubt there is much yet to learn about the Wood Duck—it is a living barometer of wetlands health and as a cavity nester is easily subject to experiment and study. Finally, I urge those contemplating such study to learn from those who have gone before, build on their strengths, correct their weaknesses, but provide future biologists with data sets that allow direct comparison with those that exist.—Jerome A. Jackson.

California Birds: Their Status and Distribution. By Arnold Small, illus. by Arnold Small and Brian E. Small. Ibis Publishing Co., Vista, California. 1994: 342 pp., 56 color plates with caption figs. $55.00 (cloth).—California is an immense state covering almost 10° in latitude with a coastline over 800 miles long and an abundance of diverse habitats ranging from moist conifer forests to arid deserts. It is hardly surprising that a state so richly endowed ecologically should harbor a high diversity of bird species, in this case 586 species recorded since 1900, of which 325 have bred at some time and 278 breed regularly. Arnold Small, one of California's best known field ornithologists, has taken it upon himself to author a book describing the often complex distribution patterns of each member of California's avifauna. This book is larger, much more detailed, and far more useful than Small's earlier volume (1974, *The Birds of California,* Winchester Press, New York). Anyone seriously interested in California birds will want to own a copy and make frequent use of it.

This is a large format (8.5 in. × 11 in.) "coffee table" sized book that can fit comfortably in one's home library or automobile but not in a day pack. However, it should really not be necessary to lug it into the field. It is an attractively produced volume with numerous insets of color plates, each plate containing six photographs (for a total of 336) in color. Most of the photographs are full frame shots of birds, although some are meant to illustrate the kinds of habitats in which the bird species on the plate are found (i.e., open ocean, tidal saltwater marshes and mudflats, brushland, the Great Basin, montane forests). The quality of the photographs is sharp, although some are rather dark, due mostly to background. However attractive, the inclusion of such a rich array of color adds little if anything to the utility of the book and undoubtedly contributes to its rather steep price.

The book is well designed to facilitate its use. California is a complex state with 58 counties, many unique natural areas (e.g., six national parks, seven national monuments, 21 national forests, dozens of state parks and beaches, etc.), and several major ecological landforms. On the front endpaper, each county is clearly located on a large map along with a list of counties and county abbreviations (used throughout the text). Putting these on the endpaper makes it very easy to refer to them from the text. The rear endpaper is a list and an excellent map of key California birding localities, also highly useful both for its thoroughness and for ease of access. The frontispiece is yet another map, this one showing major landforms. The reader will need to become familiar with each of these maps in order to understand the species distribution accounts.

The first 31 pages provide an overview of the physical environment and bird life of California. Each of California's major ecological regions is briefly discussed, followed by an account of the general nature and origins of California's birds. This account is largely focussed on discussing the phenomenon of vagrancy, with separate lists of vagrants that have appeared from the east, Mexico and/or Arizona, Asia, Alaska and/or Canada, and the Atlantic Ocean. Possible causes of vagrancy are discussed in some detail, along with migrant traps, habitat islands, and other unique habitats of special interest to birders, perhaps more

so than ornithologists. The long account of vagrancy is followed by a brief discussion of patterns of bird migration in California. Absent from Small's overview is any significant discussion of large scale changes in bird populations that have occurred during the present century, although he lists former nesters, very rare, irregular nesters, and recent nesters. Small hypothesizes that the most abundant bird species currently occurring in California may be one of the following: Sooty Shearwater (*Puffinus griseus*) [tens of millions occur offshore but within state boundaries during part of the year], European Starling (*Sturnus vulgaris*), Mourning Dove (*Zenaida macroura*), Red-winged Blackbird (*Agelaius phoeniceus*), and House Sparrow (*Passer domesticus*).

The species accounts are the most important component of the volume. Each species is discussed as to its seasonal status, habitat, and range in California. There is a code next to the name that informs with regard to degree of abundance or rarity as well as breeding status. In these accounts, Small briefly discusses any significant changes in status (e.g., for Fulvous Whistling-Duck (*Dendrocygna bicolor*), "formerly fairly common, but reduced to a rare or very uncommon summer visitor in the Imperial Valley near the south end of the Salton Sea"). In general, the species accounts are most detailed with regard to range in California. Where appropriate, Small lists estimated populations (e.g., "50,000–60,000 Tundra Swans (*Cygnus columbianus*) winter in the Central Valley"), and he provides adequate detail with regard to regional differences in occurrence within the state. This book is not meant as a bird finding guide, but the serious reader will, in fact, obtain reasonable knowledge of where to look for species of interest. For example Black Swift (*Cypseloides niger*) is given 33 lines of text detailing the various locations of colonies throughout the state. Having, within the past three years, birded during all seasons throughout much of California, I checked the species accounts against my own notes and found very close agreement. I also asked several highly experienced California birders to examine the species accounts. Each had quibbles, but each expressed the view that the accounts were in general quite accurate and useful. Some bird species such as Forster's Tern (*Sterna forsteri*), Hermit Thrush (*Catharus guttatus*) Solitary Vireo (*Vireo solitarius*), and Savannah Sparrow (*Passerculus sandwichensis*), have complex distributions within California, and Small has done a creditable job of describing the ranges of these challenging species as well as those whose distributions are less problematical.

There are supplemental species accounts that record those species that have been reported in California but are "of questionable origin, viable status, or questionable identification." There are also species accounts of exotics that are considered to be non-established releases and escapees. To round out the utility of the book, there are, following the species accounts, appendices on sources of records of California birds, the California Bird Records Committee (which determines the official state list), standard abbreviations used in the text, and a checklist of California birds. There is both a bibliography and literature cited section and an adequate index.

There is currently no other up-to-date volume that encompasses all of California's birds. Small's book is very helpful and deserves wide usage.—John C. Kricher.

Birding in Ohio. 2nd ed. By Tom Thomson. Indiana Univ. Press, Bloomington and Indianapolis, Indiana. 1994: 268 pp. $29.95 (cloth), $13.95 (paper).—This book is a guide to more than 300 Ohio birding localities. The nature of each site is described and specialty birds are listed. Sites are arranged according to region. Maps are provided which show routes and locations but not much other detail. A few black-and-white sketches are included, apparently mostly for decoration.

This book is a useful addition to regional bird-finding guides, although I much prefer the format and detail provided by Lane/ABA guides. The treatment of individual sites varies greatly but none seem to have the kind of useful bird-finding tips commonly available in books for other sites or regions. The sketches range from very beautiful to a few that are so dark as to obscure identification of the bird. Some of the maps appear to have been copied from other road maps and, in a few cases, suffered from the copy process.

The "Bibliography" is dated, not entirely in correct alphabetical order, and cites "Wilson Bull. et al., The" 1925–1980, as if the journal somehow mysteriously stopped 15 years ago! Jerry Jackson is listed as the contact person (editor?) for *The Wilson Bulletin* even though he has not been editor or an officer of the society for many years. Also, there are notations in boxes "Special regional insert," followed by "End of regional insert," also in boxes. Why these are provided is not clear.

The final section, a list of the birds of Ohio, could be more useful with detail about where and when to expect each species—especially the rarities. Other bird-finding guides have used seasonally and/or regionally arranged bar diagrams to provide much of this information. I urge the author to consider some of these revisions in a subsequent edition.—C. R. Blem.

The Birds of Michigan. By Gail A. McPeek (ed.) Indiana Univ. Press, Bloomington, Indiana. 1994:358 pp., numerous color plates. $59.95.—This book may be a disappointment to those who have seen "The Atlas of Breeding Birds of Michigan" (R. Brewer, G. A. McPeek, and R. J. Adams, Jr.; 1991. The breeding atlas was awash in information, data, and detail. The present volume is mainly a coffee table book. Individual species accounts apportioned among about 10 authors range from about one page in length to very brief paragraphs (for extreme rarities). Individual coverage varies, ranging from accounts that consider (in a general way) breeding, vocalizations, abundance, and habitat preference. However, the sort of detail that many ornithologists can actually use and often prefer (e.g., real clutch size data, not estimates; migration dates, data on geographic variation) was omitted, perhaps as a sacrifice to the space taken by the color plates.

The color plates were done by five artists and vary widely in composition and quality. Some paintings seemingly were not cropped properly; parts of birds are chopped off at the edge of the page, or the bird overwhelms the page because of size format. A few plates are not of the quality one would expect of a book of this type. Some birds looked more like mounted specimens than living organisms. Particularly attractive plates were done by John Felsing (in a form reminiscent of Sutton) and David Mohrhardt. The binding and printing are very attractive and nicely done. There were no obvious typographic or editorial errors. A reasonable bibliography is provided.

I use this last paragraph to encourage editors and printers of state and regional bird texts to use their opportunity to produce works less given to color plates and more to real data. I know that the "pretty" book is likely to sell more copies, but please try to strike a balance in which the real meat of the science is not lost in an attempt to be popular. We get few chances to produce definitive state books and to educate the public about ornithology. I urge those writing texts to keep this in mind and to resist the pressure to write "general" books with little new, precise information. The process of educating the public without being too general ("dumbing down" some have called it) is difficult but worth the effort in behalf of the science of ornithology.—C. R. Blem.

THE BIRDLIFE OF FLORIDA. By Henry M. Stevenson and Bruce H. Anderson. University Press of Florida, Gainesville, Florida. 1994:892 pp. $120.00.—This volume represents the life work of the senior author who checked all museum specimens and compiled records for more than 40 years. The book is a rich source of information on Florida birds. It includes maps of their distribution and provides detailed descriptions of status, relative abundance, migration, breeding, adverse factors, habits and habitat, and problems of identification. An exhaustive reference section is included. The binding and format are excellent, and the book is attractive, but the scholarly approach used in this book may not be attractive to the casual birder. For example, the lack of drawings or color plates may hinder sales, but to my way of thinking, this is the way state books should be done. I have spent a good deal of time birding in Florida, but I learned something in the discussion of every species in this book. The book is, unfortunately, fairly expensive for reasons not obvious to me.—C. R. BLEM.

INFORMATION FOR AUTHORS

The Wilson Bulletin publishes significant research and review articles in the field of ornithology. Mss are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

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Authors of accepted papers are urged to submit voucher photographs of their work to

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This issue of *The Wilson Bulletin* was published on 1 September 1995.

The Wilson Bulletin

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CONTENTS

MAJOR PAPERS

ARTIC FOX INFLUENCE ON A SEABIRD COMMUNITY IN LABRADOR: A NATURAL EXPERIMENT ..... *T. R. Birkhead and D. N. Nettleship* 397

MIGRATION CHRONOLOGY, SEX RATIO, AND BODY MASS OF LEAST SANDPIPERS IN BRITISH COLUMBIA ..... *Robert W. Butler and Gary W. Kaiser* 413

COMMON TERNS NESTING ON NAVIGATIONAL AIDS AND NATURAL ISLANDS IN THE ST. LAWRENCE RIVER, NEW YORK ..... *Kenneth Karwowski, J. Edward Gates, and Lee H. Harper* 423

FORAGING SOCIABILITY OF NESTING WADING BIRDS (CICONIIFORMES) AT LAKE OKEECHOBEE, FLORIDA ..... *Jeff P. Smith* 437

DISTRIBUTION AND ABUNDANCE OF RAPTORS IN PUERTO RICO ..... *Frank F. Rivera-Milán* 452

BIRD SPECIES RICHNESS IN RELATION TO ISOLATION OF ASPEN HABITATS ..... *Gail M. Turchi, Patricia L. Kennedy, Dean Urban, and Dale Hein* 463

BREEDING BIOLOGY OF FLORIDA PRAIRIE WARBLERS AND CUBAN YELLOW WARBLERS ..... *John W. Prather and Alexander Cruz* 475

ARTHROPOD PREY OF NESTLING RED-COCKADED WOODPECKERS IN THE UPPER COASTAL PLAIN OF SOUTH CAROLINA ..... *James L. Hanula and Kathleen E. Fanzreb* 485

THE CALLS AND ASSOCIATED BEHAVIOR OF BREEDING WILLOW PTARMIGAN IN CANADA ..... *Kathy Martin, Andrew G. Horn, and Susan J. Hannon* 496

NATURAL HISTORY OF THE MONK PARAKEET IN HYDE PARK, CHICAGO ..... *Jeremy Hyman and Stephen Pruett-Jones* 510

SUCCESSFUL NESTING BEHAVIOR OF PUERTO RICAN PARROTS ..... *Karen A. Wilson, Rebecca Field, and Marcia H. Wilson* 518

LIFE HISTORY AND ECOLOGY OF FLAMMULATED OWLS IN A MARGINAL NEW MEXICO POPULATION ..... *D. Archibald McCallum, Frederick R. Gehlbach, and Sophie W. Webb* 530

SHORT COMMUNICATIONS

THE EFFECTS OF EXOGENOUS TESTOSTERONE ON MALE NORTHERN MOCKINGBIRDS DURING THE BREEDING SEASON ..... *Michael J. Justice and Cheryl A. Logan* 538

EFFECTS OF FOOD SUPPLEMENTATION AND PREDATOR SIMULATION ON NUTHATCHES AND PARIDS WITHIN MIXED-SPECIES FLOCKS ..... *Peter H. Yaukey* 542

MALLARD-LIKE DUCKS IN THE PLAYA LAKES REGION ..... *Alan M. Fedynich and Olin E. Rhodes, Jr.* 548

FIRST DESCRIPTION OF THE NEST AND EGGS OF THE SOCORRO MOCKINGBIRD ..... *Juan E. Martínez Gómez and Robert L. Curry* 551

EXCEPTIONAL RESPONSE BY FEMALE RED CROSSBILLS TO DIETARY CAROTENOID SUPPLEMENTATION ..... *Geoffrey E. Hill and Craig W. Benkman* 555

WINTER FOOD OF A SMALL INSECTIVOROUS BIRD, THE GOLDEN-CROWNED KINGLET ..... *Bernd Heinrich and Ross Bell* 558

FIRST NESTING RECORD OF THE GREAT-TAILED GRACKLE IN OREGON ..... *Eric J. Scheuering and Gary L. Ivey* 562

GROUND-NESTING LONG-EARED OWLS ..... *Michael T. Maples, Denver W. Holt, and R. Wayne Campbell* 563

GRAY FLYCATCHER PREDATION ON A HUMMINGBIRD ..... *Gilles Seutin and Victor Apanius* 565

ORNITHOLOGICAL LITERATURE 568

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 107, NO. 4 DECEMBER 1995 PAGES 577–814

(ISSN 0043-5643)

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THE WILSON BULLETIN

(ISSN 0043-5643)

THE WILSON BULLETIN (ISSN 0043-5643) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Second-class postage paid at Lawrence, KS. POSTMASTER: Send address changes to THE WILSON BULLETIN, P.O. Box 1897, Lawrence, KS 66044-8897.

Back issues or single copies are available for $12.00 each. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

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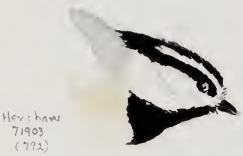

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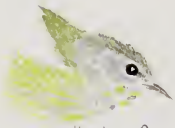
Mt. Chickadee

Burleigh 365530

Sulphur-bellied Flycatcher

V. Bailey 240853

Arizona Woodpecker



Henshaw ♀ juv 69253 (256)

Orange-crowned Warbler

Levy 482318

Spotted Owl

Henshaw 79525

Brown-throated House Wren

Holt 258633

Yellow-eyed Junco

Pygmy Owlet

Pygmy Owl

JTM Burma field notes and Abbott 181726

Glaucidium brodiei

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Tom Burleigh 411997 and Fitt 272381

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Webb Hawk Graham Heliograph Ladybug

Mt. Graham, from an airplane, due south

Joe Marshall 1991

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 107, NO. 4 DECEMBER 1995 PAGES 577–814

Wilson Bull., 107(4), 1995, pp. 577–589

NEOTROPICAL MIGRANTS IN UNDISTURBED AND HUMAN-ALTERED FORESTS OF JAMAICA

JOHN L. CONFER[1] AND RICHARD T. HOLMES[2]

ABSTRACT.—Neotropical migrant birds were censused in a variety of natural and human-altered habitats in Jamaica, West Indies. Although power analyses indicated that only differences in abundance >50% were likely to be detected with available sample sizes, we found that total migrant abundance was significantly greater in mangrove and coastal forests than in wet or dry limestone forests. There was no detectable decrease in the total number of Neotropical migrant birds within each forest type as plant biomass decreased with human activity. Species replacements, however, did occur. Common Yellowthroats (*Geothlypis trichas*) increased and other species such as American Redstart (*Setophaga ruticilla*) decreased as vegetation decreased. These results indicate that as a group migrant birds wintering in Jamaica have a wide tolerance for habitat disturbance, but that individual species have specific habitat requirements. Thus, the relative availability of different habitats will affect the abundance of each species. *Received 23 Sept. 1994, accepted 15 May 1995.*

Recent declines in breeding populations of migratory songbirds in North America have been attributed largely to changes in habitat, either in temperate breeding areas or in tropical wintering sites, or in both (Robbins et al. 1989; Askins et al. 1990; Finch 1991; Sherry and Holmes, in press). Winter habitat has been most often implicated in these declines, probably because of the rapidity with which these areas have been deforested in the last two to three decades (Terborgh 1989). This has led to increased interest in the patterns of habitat use by migrants birds during their time in the Neotropics (Keast and Morton 1980, Hagan and Johnston 1992). In particular, it is important to know which habitats these migrant species occupy, their densities, and how their distributions are affected by changes or modifications in habitat due to human activity.

Several recent studies have considered these questions for migrants in

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the Caribbean and in Central America. In the Virgin Islands, Askins et al. (1992) found relatively few migrants in areas where forests had been severely degraded or converted to gardens or forest fragments. In contrast in the Yucatan, Lynch (1992) found comparable numbers and relative abundances of migrant species in areas with traditional forms of agriculture as in natural habitats, but relatively few in pastures created for cattle. In the Greater Antilles, Belize, and Costa Rica, Robbins et al. (1992) also found migrants in plantations of cacao, citrus or coffee, which provided a significant amount of canopy cover and presumably the necessary food resources. In an extensive sampling program in the Caribbean, Wunderle and Waide (1993) showed that some Neotropical migrant species were specialists of mature forests, others used a wide variety of habitats, yet others were specialists of disturbed habitats. The differences observed among these surveys suggests that a thorough assessment of winter habitat for Neotropical migrants requires knowledge for each region.

In this study, we examined the distribution and relative abundance of migrant landbirds during March 1992 in a series of natural and human-altered habitats in Jamaica, W.I. We censused migrants in four kinds of natural forests (dry limestone, wet limestone, coastal, and mangrove) and in several human-altered habitats derived from each of these formations. Differences in bird abundances between natural and derived habitats help assess human impact on the distribution and carrying capacity for these species in Jamaica.

METHODS

Neotropical migrants were censused in widely scattered locations in the western two thirds of Jamaica (west of latitude 76°55′). This region was selected because of concurrent use of satellite imagery to assess vegetation patterns (Confer et al. unpubl. data). We used point counts to estimate bird abundance. All counts were made between 2–29 March 1992, either in the morning (~06:15 to 11:00) or in late afternoon (~16:00 until dark). To reduce the probability of counting the same individual twice, we spaced point counts at ≥100 m intervals in densely wooded areas as did Wunderle and Waide (1993). Hutto et al. (1986) recommended ≥200 m intervals, which we adopted only in open areas such as pasture. Sliwa and Sherry (1992) observed that migrants wintering in Jamaica did not cross territorial boundaries in response to playbacks, and that both American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*Dendroica caerulescens*) were hyper-dispersed as expected for territorial birds. Furthermore, we obtained more than 50 point counts from four study plots in which more than 75 winter resident Neotropical migrant birds were distinctively color marked (R. T. Holmes and T. W. Sherry, continuing research). Only once was the same banded individual recognized at two consecutive point counts, which shows that replicate counting occurred rarely with point counts 100 m apart in heavily wooded habitat. Moreover, most Neotropical migrant birds in Jamaica occur alone, and rarely in flocks (Lack 1976, Holmes et al. 1989), so that replicate counting of birds for that reason was unlikely.

To detect the maximum number of nearby birds, we used taped calls interspersed with "spshing" (Smith 1975) in the following pattern for each count: 1 min of initial silence –

2 min of tape playback of American Redstart song and chip notes –1 min of spshing –2 min of silence –2 min of Black-throated Blue Warbler song and chip notes –1 min of spshing –1 min of silence. Segments of tapes used by Sliwa and Sherry (1992) were duplicated for playback. Sliwa and Sherry showed that playbacks increased the detection of American Redstarts and Black-throated Blue Warblers by 300 and 230%, respectively, and enhanced the count of some other warbler species. Our emphasis on American Redstarts and Black-throated Blue Warblers complements continuing studies of their winter ecology in Jamaica (Holmes et al. 1989, Holmes and Sherry 1992, R. T. Holmes and T. W. Sherry unpubl data). The attraction of birds to spshing has been documented (Smith 1975), and is well known to birders. Spshing was as loud as possible when no birds were in sight and was reduced as birds approached.

A preliminary list of potential study sites in coastal, mangrove, wet limestone, and dry limestone forests was determined based on descriptions in Asprey and Loveless (1958), Asprey and Robbins (1953), Lack (1976), Loveless and Asprey (1957), Sliwa and Sherry (1993), Wunderle and Waide (1992), and our own field experience in Jamaica. The distribution of Neotropical migrant birds in Jamaica varies with elevation and especially rainfall (Lack 1976, Wunderle and Waide 1993). Thus, to obtain a representative sample of bird abundance, we selected sites with the widest possible range of rainfall and elevation within each habitat type as well as those with intermediate conditions. Rainfall estimates were based on records for December, January and February, the three months preceding the census. Winter is the dry season in much of the Caribbean including Jamaica, and may be a time of food shortage for migrants as discussed by Wunderle and Waide (1993) and as studied in Jamaica by Parrish and Sherry (1994). Census areas in the same forest type were at least 15 km apart. Census points were located at least 50 m from an ecotone, except in a few narrow mangrove and coastal forest stands where they were only 15–25 m from the edge.

Human impact on the density of vegetation was estimated subjectively. At each census point, the density of vegetation was compared visually with that of similar but undisturbed habitat types, and was categorized as follows: 1 = less than 2% reduction in the maximum vegetation caused by humans and their livestock, 2 = 2–33% reduction, 3 = 33–66% reduction, 4 = 67–100% reduction. The biomass at point counts in agricultural or grazed areas was compared to the biomass of natural areas without regard to species composition. For example, coffee plantations were estimated to have 33–66% of the biomass of the original wet limestone forest (categories 2 or 3) even though few of the original plant species were present. Visual estimates were the only feasible method even though they may not as quantitative or as accurate as other more time-intensive methods. Previous use of visual estimates of biomass have been shown to provide sufficient statistical power to discriminate between the similar nesting habitat of Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*V. chrysoptera*) (Confer and Knapp 1981).

A total of 122 point counts was obtained from ten mangrove forest study areas in pure and mixed stands of red (*Rhizophora mangle*), white (*Laguncularia racemosa*), and black (*Avicennia germinans*) mangroves. Most counts were obtained in areas with a canopy height that ranged between 5–15 m: others were in an area with a red mangrove canopy which exceeded 25 m. Black and especially white mangroves grew in higher and drier areas than red mangrove sometimes with stunted and very sparse growth. Some sites contained downed trees, most of which resulted from Hurricane Gilbert in September 1988. Five census counts were on a dike which separated undisturbed forest from a forest completely destroyed by ongoing development. These sites with 50% cover reduction were assigned a human impact value of 3. The total number of counts in each category of human impact, 1–4, was 48, 38, 26, and 10, respectively. No counts were obtained in areas where virtually all mangrove

vegetation had been eliminated. A total of 105 point counts was obtained at four census areas of wet limestone forest and in nearby pasture and in plantings of coffee, yams, banana, and coconut that had once been wet limestone forest. In forested areas, current human influence was restricted to selective removal by hand of a few trees, which had a minor impact on the canopy. Canopy of wet limestone forest ranged up to 40 m, and vines and epiphytes were abundant. Point counts in the valleys were located in pasture land and agricultural plantings, and some included small clusters of trees or wooded fence rows. The number of counts in each category of human impact, 1–4, was 34, 17, 8, and 46, respectively. We counted birds at 112 points in five census areas of dry limestone forest. Ten xeric sites had a cactus, thorn-scrub community (Asprey and Robbins 1953) dominated by columnar cactus (*Stenocereus hystrix*) and thorn acacia (*Acacia tortuosa*). Evergreen seasonal forest (Beard 1944) with a canopy to 20 m, having some foliage reduction during the dry season and abundant lianas and epiphytes occurred at the least xeric sites. Overgrazing and cutting of forests for firewood was widespread, producing scrub, or ruinate, habitat in areas probably once forested. In most disturbed sites the dominant vegetation was thorn acacia occasionally mixed with columnar cactus. For the four categories of human impact, 1–4, the number of counts was 43, 17, 28, and 24, respectively. We made 15 counts at five areas in coastal forests on slight elevations characterized by a wide variety of plant associations. These frequently were dominated by palms (*Sabal jamaicensis*) and logwood (*Haematoxylon campechianum*) and other shrubby vegetation, along with stands of taller trees such as red birch (*Bursera simaruba*) and burnwood (*Metopium brownii*). At several sites, coastal forests graded into mangrove forests or dry limestone forests, and some birds may have moved among these habitats.

Statistical tests were performed with SYSTAT®, excepting a few chi-square tests. Group comparisons were screened for homogeneity of variances with Bartlett's test. If the variances were not homogeneous, the data were transformed by log, square root, or arc-sine functions. If the initial or transformed variances were homogeneous, tests for differences among groups used a one-way ANOVA. The sum probability of a Type I error for all group comparisons was set at 5% with a Tukey-Kramer adjustment for unequal sample size. If variances remained significantly different despite transformation, we used Kruskal-Wallis or Mann-Whitney *U*-tests. Comparisons of bird abundance among categories of human-caused reduction in vegetation used data pooled for category 1–3 to obtain larger sample sizes. Differences in abundance between the pooled counts and point counts at category 4 were tested with a Student's *t* statistic. Power analyses (Cohen 1987) of the data were performed to determine the ability of our data to detect significant differences (see below).

RESULTS

A total of 704 Neotropical migrant birds of 16 species observed at 354 point counts averaged 2.0 individuals per point. Paruline warblers comprised >99% of the migrants. Six species were observed at more than 50 points (Fig. 1): American Redstart (162 individuals), Prairie Warbler (*Dendroica discolor*) (101), Northern Waterthrush (*Seiurus noveboracensis*) (89), Black-and-White Warbler (*Mniotilta varia*) (68), Black-throated Blue Warbler (58), and Common Yellowthroat (75). Other species were Northern Parula (*Parula americana*) (55), Palm Warbler (*D. palmarum*) (28), Magnolia Warbler (*D. magnolia*) (14), Cape May Warbler (*D. tigrina*) (12), Worm-eating Warbler (*Helmintheros vermivorus*) (10), Ovenbird (*Seiurus aurocapillus*) (6), Prothonotary Warbler (*Protonotaria ci-*

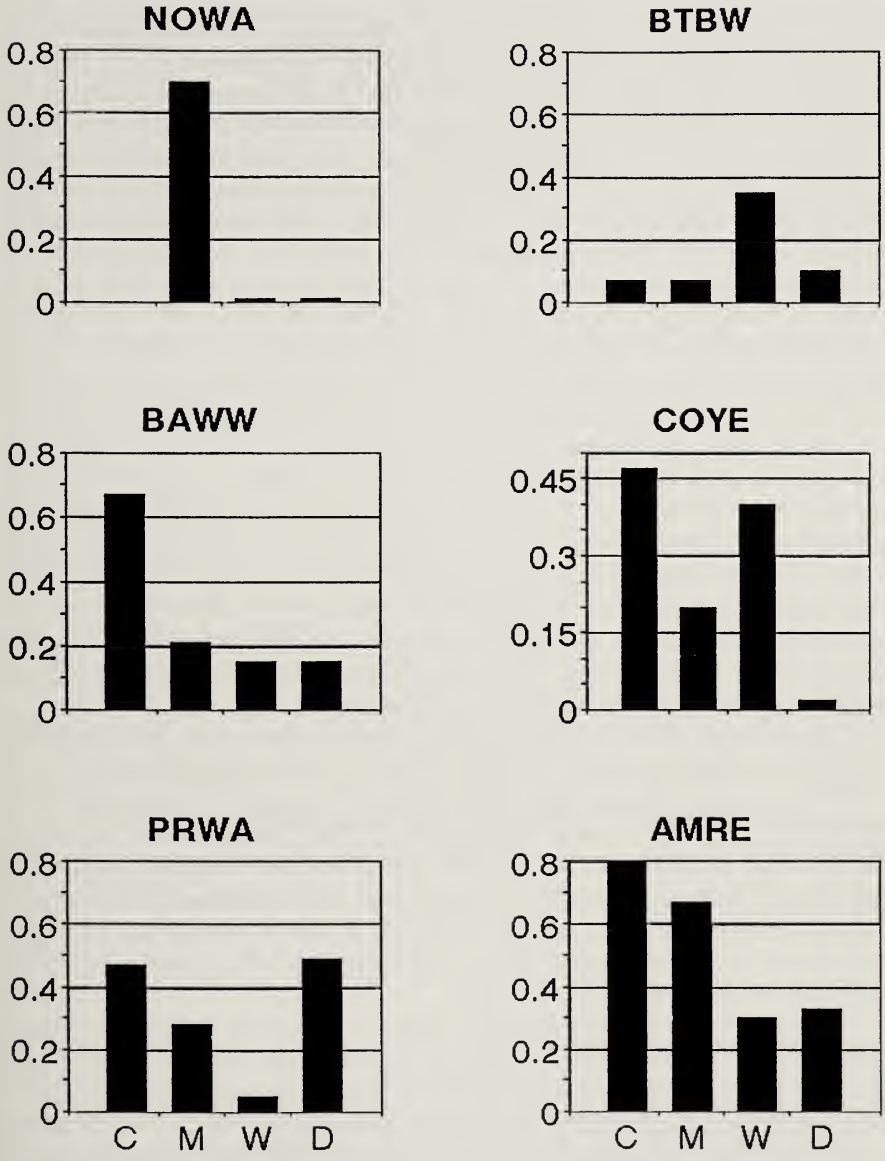

FIG. 1. Distribution of some common Neotropical migrant birds in Jamaica. Values are the mean of all point counts in each of four forest types. C = coastal; M = mangrove; W = wet limestone; D = dry limestone forests; NOWA = Northern Waterthrush; BTBW = Black-throated Blue Warbler; BAWW = Black-and-white Warbler; COYE = Common Yellowthroat; PRWA = Prairie Warbler; and AMRE = American Redstart. Note change of scale for COYE.

trea) (3), Indigo Bunting (*Passerina cyanea*) (2), Yellow-throated Vireo (*Vireo flavifrons*) (1), Hooded Warbler (*Wilsonia citrina*) (1).

Many of our comparisons were based on small sample size and showed only minor differences between means, increasing the chances of a Type II statistical error. A power analysis of our data used the number of migrants detected per point count for human impact categories 1–3 pooled vs category 4 for the three forest types with >100 point counts (coastal forests excluded). Power analyses of the difference in total number of Neotropical migrants among the forest types showed a 46–88% probability of detecting a true difference of ≥50% (Table 1). A 30% difference in total Neotropical migrant birds would be detected as significant in less than 10% of similar trials. Comparisons of individual species involved far fewer individuals per point count, and the power analyses show that for these data a difference of 50% was likely to be detected only for sample sizes of many hundreds to thousands of point counts. No studies to date have achieved such sample sizes for a within-habitat analysis of the effect of human disturbance on migrant bird abundance. Our sample sizes of 105–122 point counts of total Neotropical migrants for each habitat may be as sensitive as previous studies but are likely to detect a statistically significant difference only for true differences ≥50% (see Discussion). Tests for individual species are likely to show a difference only for major changes in relative abundance.

The total number of Neotropical migrant birds per point count for both mangrove forests (mean ± *SE* 2.53 ± 0.17), and coastal forests (3.67 ± 0.58) were significantly higher than those for wet limestone forests (1.43 ± 0.11) or dry limestone forests (1.70 ± 0.16) (Tukey-Kramer one-way ANOVA, $P < 0.01$). The total number of Neotropical migrant birds were indistinguishable for mangrove forests and coastal forests and for wet limestone forests and dry limestone forests. Coastal forests had the highest counts of Neotropical migrant birds, but the sample size was small and the variance high.

Northern Waterthrushes occurred almost exclusively in mangrove forests (Fig. 1), as observed by others (Wunderle and Waide 1993). They were the most habitat-specific species detected at more than 50 point counts. Most waterthrushes occurred within sight of water. Our censuses were conducted at the end of the dry season by which time standing water was visible at only 63% (N = 82) of the mangrove forest point counts. The mean number per point count with and without water was 0.99 and 0.22, respectively, a highly significant difference ($t = 5.835$, $P < 0.001$, after square-root transformation).

American Redstarts were common in all forest types (Fig. 1), although their densities in mangrove and coastal forests were significantly higher

TABLE 1

DETECTION OF HUMAN INFLUENCE ON BIRD ABUNDANCE

Habitat	Calculated[a,b]	Bird species[c] NTMB	PRWA	BAWW	AMRE	COYE	BTBW
Mangrove forests							
For 30% change and							
observed N = 113 and 9	Power:	0.20	0.08	—	0.12	<0.06	<0.06
observed variance and power = 0.9	N:	132	>1000	—	350	>1000	>1000
observed variance and power = 0.8	N:	99	980	—	240	>1000	>1000
For 50% change and							
observed N = 113 and 9	Power:	0.46	0.11	—	0.25	0.07	0.07
observed variance and power = 0.8	N:	38	262	—	82	1335	1335
Dry limestone forests							
For 30% change and							
observed N = 85 and 27	Power:	0.32	0.15	0.10	0.17	—	—
observed variance and power = 0.9	N:	210	540	>1000	470	—	—
observed variance and power = 0.8	N:	160	390	>1000	360	—	—
For 50% change and							
observed N = 85 and 27	Power:	0.66	0.33	0.16	0.38	—	—
observed variance and power = 0.80	N:	58	145	371	122	—	—
Wet limestone forests							
For 30% change and							
observed N = 59 and 46	Power:	0.40	<0.08	0.08	0.13	0.1	0.2
observed variance and power = 0.9	N:	160	>1500	>1500	>1000	>1500	500
observed variance and power = 0.8	N:	122	>1500	1600	980	1340	360
For 50% change and							
observed N = 59 and 46	Power:	0.88	<0.08	0.10	0.26	0.17	0.44
observed variance and power = 0.8	N:	43	>1000	621	284	393	129

[a] The calculated power is the probability of detecting a specified change at the 95% confidence level comparing highly disturbed sites to all others given the observed sample sizes.
[b] The calculated N is the number of counts, equally divided between highly disturbed sites and all others, necessary for the specified probability of detecting a specified change at the 95% confidence level given the observed variance.
[c] NTMB = Neotropical migrant birds; PRWA = Prairie Warbler; BAWW = Black-and-white Warbler; AMRE = American Redstart; COYE = Common Yellowthroat; BTBW = Black-throated Blue Warbler.

than in wet or dry limestone forests (Tukey-Kramer one-way ANOVA of ln transformed data, $P < 0.05$). Black-and-white Warblers were widespread, but occurred in significantly greater density in coastal forests than in any other habitat (Tukey-Kramer one-way ANOVA of ln transformed data, $P < 0.05$). Chi-square 2×3 contingency analyses showed significant differences in frequency of detection among forest types for the following species: Common Yellowthroats, rare in dry limestone forests (chi square = 49, $P < 0.001$); Prairie Warblers, rare in wet limestone forests (chi square = 29, $P < 0.001$); and Black-throated Blue Warblers, moderately abundant only in wet limestone forests (chi square = 37, $P < 0.001$) (Fig. 1).

Our observations of the differences of bird density with respect to human-caused reduction of vegetation suggest that only sites with extreme disturbance are likely to have significant reductions in bird abundance (Fig. 2), while the power analyses suggested that only comparisons among large samples would be likely to detect any difference. Consequently, we pooled results for category 1–3 and compared these to category 4.

Human influence had little effect on total Neotropical migrants per point count within each major habitat (Fig. 2). The coefficient of variation for each forest type derived from the means of the total number of Neotropical migrants for each category of human influence varied by only 6.0–18.6%. *t*-tests showed no significant difference in total Neotropical migrant birds between categories 1–3 combined and category 4 for each forest type.

Point counts for mangrove forests at sites with very little vegetation (category 4) still had a large total number of migrants (Fig. 2). However, mangrove point counts could not be obtained in areas that were totally denuded because construction activities prevented access. We believe paruline warblers would have been extremely rare in such sites. None of the six most common species had a detectable difference in abundance in mangrove forests when categories 1–3 were pooled and compared with category 4 ($P > 0.05$). Black-and-white Warblers were the only species that showed a decline in moderately disturbed mangrove; chi-square analysis of all four categories for Black-and-white Warblers showed a highly significant difference (chi square = 17, df = 3, $P < 0.001$).

Human impact in areas of former wet limestone forests produced a heterogeneous habitat including a very diversified agriculture. The total number of Neotropical migrants was statistically indistinguishable comparing categories 1–3 with category 4 ($P > 0.05$). Some category 4 counts in areas which were not denuded and which had a forest edge, actually had a high density of Neotropical migrant birds. Among individual species, American Redstarts declined ($t = 2.18$, $P = 0.032$ using square-root

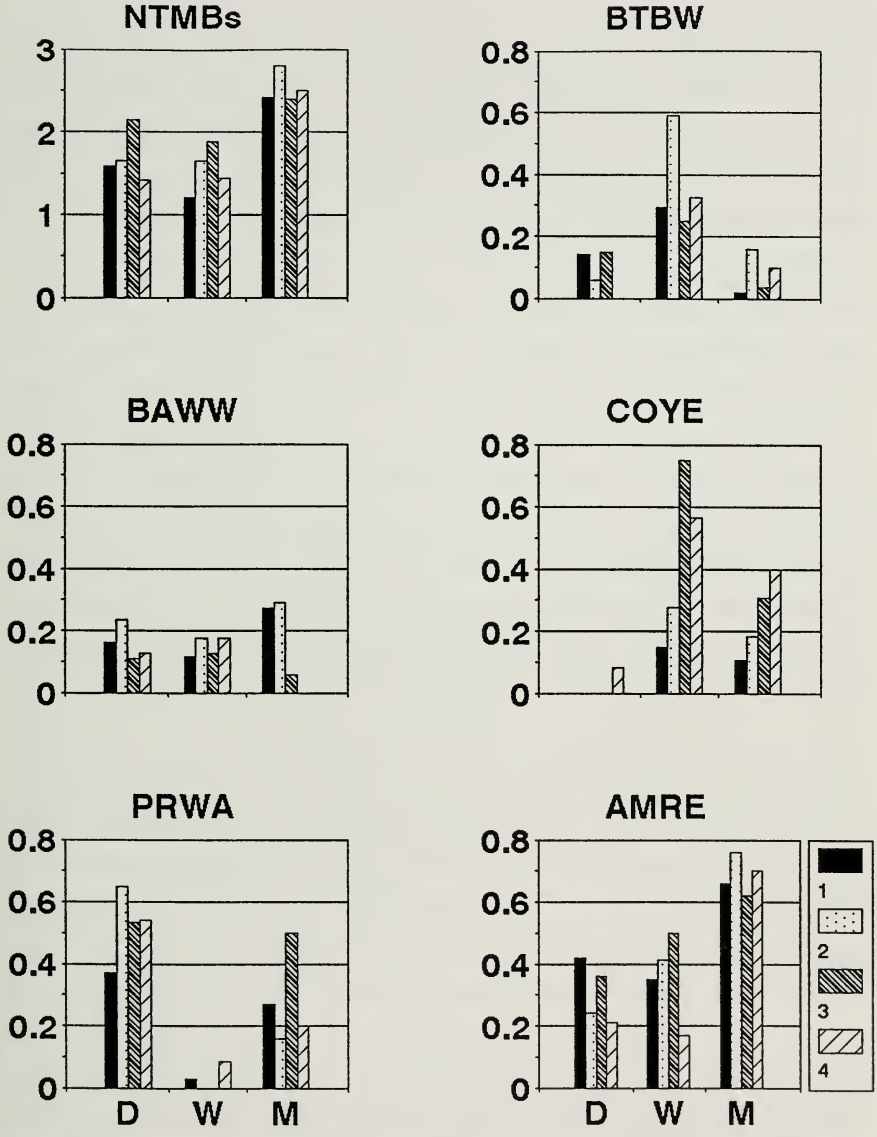

FIG. 2. Distribution of Neotropical migrant birds related to human disturbance. Histograms show mean abundance per point count for four categories of human impact for each of three habitats. NTMBs = Neotropical migrant birds. Other abbreviations and categories as in Fig. 1. Note change of scale for NYMBs.

transformation) and Common Yellowthroats increased ($t = 2.214$, $P = 0.029$) comparing point counts with the most extensive reduction in biomass to all others. Sliwa and Sherry (1993) observed that the detection of Common Yellowthroats was decreased by taped playbacks of American Redstarts and Black-throated Blue Warblers. However, we observed that spshing produced responses from many birds which were undetected until spshing started, especially Common Yellowthroats.

Human impact on dry limestone forest seemed to be greater than for any other habitat in our study areas. Eight counts were taken in areas with nearly a 100% reduction in biomass due to housing construction or extreme cutting plus overgrazing. No Neotropical migrant birds were observed during these counts. Despite the absence of Neotropical migrant birds under these extreme conditions, when these counts are pooled with other category 4 counts with little vegetation, no effect of human activity on total Neotropical migrant birds was detected ($t = 0.896$, $P = 0.372$). Two species that occurred at ≥50 point counts showed an absolute difference in abundance related to human impact on dry limestone forest. Black-throated Blue Warblers were present only in category 1–3, whereas Common Yellowthroats were present only in category 4. But with their infrequent occurrence and resultant small sample size, these differences were not statistically significant (chi-square, $P > 0.05$).

DISCUSSION

Few of our comparisons showed significant differences in abundance of Neotropical migrants related to the extent of habitat alteration caused by human activity. Two sampling factors probably contributed to this result (1) the sampling protocol, and (2) the limited statistical power of point counts. Our category 4 areas could have as much as ⅓ the biomass of undisturbed habitat. Some locations with a biomass of slightly less than ⅓ the original still had high counts of Neotropical migrant birds. Although sites denuded of vegetation contained few if any birds, category 4 sites as a whole did not show a decline in total number of Neotropical migrant birds. Furthermore, our sampling did not distinguish among the different kinds of crops or agricultural practices. Significant differences in bird distribution among different types of agriculture have been recorded elsewhere (Wunderle and Waide 1993). Documentation of such differences in Jamaica requires additional study with an alternative sampling design. The power analyses showed that comparisons within a single species have little ability to detect differences in abundance (Table 1). Only sample sizes of several hundred to over a thousand point counts, depending on the amount of change in abundance, were likely to show statistical significance. The limitations revealed by power analyses for our

data provide insight about the statistical sensitivity of other studies that also used point counts to study Neotropical migrant birds. For our counts of Neotropical migrants, the coefficients of variation in mangrove forests, dry limestone forests, and wet limestone forests were <1. Wunderle and Waide (1992) observed fewer Neotropical migrant birds per point count with higher standard deviations and coefficients of variations >2. Thus, their data had less power than ours for the same sample size. Our results more closely approximate those of Sliwa and Sherry (1993) who reported a coefficient of variation less than one using playback recordings to sample American Redstarts and Black-throated Blue Warblers. Studies that use playbacks may obtain a more accurate census of territorial and hyperdispersed birds, reducing the variance and increasing the statistical power of the test.

While acknowledging the sampling limitations described above, we believe the results of this study indicate clearly that Neotropical migrant birds as a group occur widely in many habitats in Jamaica, including second growth, agricultural areas and other areas modified by human activity. Migrants were present in virtually every habitat that contained shrubby or woody vegetation and hence provided cover and food. Different species, however, preferentially occupied different habitats, e.g., American Redstarts were most common in mangroves, Black-throated Blue Warblers in undisturbed wet limestone forests, Common Yellowthroats in disturbed wet limestone forests, Prairie Warblers in dry limestone forests, and Northern Waterthrush in wet mangrove forests. Some species increased in abundance as forest canopy was thinned. Common Yellowthroats, in particular, increased in all three major forest types, although this increase was significant only in wet limestone forests. Palm Warblers, although too rare for analysis, occurred exclusively in category 4 point counts in all three major forest types, whereas none was recorded at any point with more vegetation. During casual observations, we noted Palm Warblers in disturbed habitats throughout Jamaica, as did Wunderle and Waide (1993).

These findings indicate that Neotropical migrants as a group have a wide tolerance for habitat disturbance, but that different species respond in different ways. Thus, as vegetation is reduced but not eliminated, habitat for Common Yellowthroats and perhaps Palm Warblers increases, while that for Black-and-White Warblers and Black-throated Blue Warblers decreases. The relative proportions of such habitats will determine the abundances of these species in their wintering areas. Conservation efforts will need to take such species-specific habitat requirements into account when developing management plans.

Point counts reveal only the patterns of abundance of migrant birds

among habitats. Abundance, however, might not either reflect survivorship in each habitat throughout the winter (van Horne 1983, see Sherry and Holmes, in press), or the ability of each habitat to prepare birds for northward migration. Different habitats, especially degraded ones, may be less suitable in terms of providing sufficient cover for overwinter survival or food. Further studies are needed to examine habitat-specific survival rates and other measures of fitness in migrant birds in winter. Such information will be useful in evaluating the long-term effects of habitat destruction and degradation on migrant bird populations and for developing conservation plans.

ACKNOWLEDGMENTS

The Petroleum Company of Jamaica, Paradise Park LTD (T. Clark), the PWD Gun and Sporting Club (E. Zaidie), and Discovery Bay Marine Lab (J. Woodley) kindly gave us permission to work on their properties. The Suttons of Marshall's Pen and the Williams of Kew Park provided much useful information about habitats and access to several study sites. The Jamaican Meteorological Service (Mr. P. Brown) and the Jamaican Survey Department (Mr. Ximines) provided data and maps. The Natural Resources Conservation Authority (Y. Strong) provided information about study sites. We thank G. Forrester for assistance with statistical analyses, L. O'Bryan and D. Coker who participated in the field work, and P. Marra, T. Sherry and P. Allen for their comments on the manuscript. Financial support was provided by a Mid-Career Fellowship from the National Science Foundation to JLC, and National Science Foundation Grants to Dartmouth College (RTH) and Tulane Univ. (T. W. Sherry).

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Wilson Bull., 107(4), 1995, pp. 590–602

AN EXPERIMENTAL STUDY OF NEST PREDATION IN A SUBTROPICAL WET FOREST FOLLOWING HURRICANE DISTURBANCE

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Abstract.—We used artificial nest experiments to study rates and patterns of egg predation in subtropical wet and lower montane wet forest on the island of Puerto Rico. Levels of depredation were higher for ground nests than for elevated nests, but we found no difference in rates of egg predation between forest edge (5–50 m) and forest interior (100–250 m) nests. We quantified 25 forest vegetation variables surrounding ground and elevated, forest interior nests, and correlated nest success with these vegetation parameters. Utilizing discriminant function analysis, nest success was correctly classified in 59% of cases (for ground nests) using two vegetation variables (shrub density and vegetation in the 2.5–3.0 m foliage height class), and in 71% of cases (for elevated nests) using six vegetation variables (canopy cover, vegetation in the 0–0.5, 0.5–1.0, 1.0–1.5, and 3.0–4.0 m foliage height classes, and *Cecropia* tree density). Our data suggest that the absence of an induced edge effect is the result of the creation of canopy openings and early successional vegetative associations in a matrix across the forest following hurricane disturbance in 1989. Comparative data suggest that the high rates of egg predation recorded here may be typical for insular forest habitats. *Received 21 Oct. 1994, accepted 15 May 1995.*

Sinópsis.—Usamos la experimentación con nidos artificiales para estudiar las razones y patrones de la depredación de los huevos en un Bosque Subtropical Húmedo y en un Bosque Montañoso Bajo Húmedo en la isla de Puerto Rico. Los niveles de depredación fueron mayores en los nidos puestos en el suelo que aquellos que estaban elevados, pero no encontramos diferencias en la razón de depredación entre los nidos que estaban en el linde del bosque (5–50 m) o en el interior (100–250 m). Cuantificamos 25 variables de la vegetación en los nidos del interior del bosque -elevados y en el suelo- correlacionando el éxito del nido con estos parámetros de vegetación. Utilizando un análisis de función discriminante, el éxito del nido fue correctamente clasificado en el 59% de los casos (para los nidos en el suelo) usando dos variables (la densidad de arbustos y la vegetación en la clase de altura de 2.5–3.0 m), y en un 71% de los casos (para los elevados) usando seis variables (la cobertura del dosel, la vegetación en las clases de altura de 0–0.5, 0.5–1.0, 1.0–1.5, y 3.0–4.0 m, y la densidád de *Cecropia*). Nuestra data sugiere que la ausencia de un efecto inducido por el borde del bosque es el resultado de la creación de aberturas en el dosel y de tempranas asociaciones susecionales de la vegetación en una matriz a través del bosque luego de las altraciones causadas por un huracán en 1989. Data comparativa sugiere que los altos grados de depredación registrados aquí pudieran ser típicos de los hábitats de bosques insulares.

Forest edges have negative impacts on a diversity of forest interior bird species (reviewed in Yahner 1988, Paton 1994). This is particularly evi-

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dent in experiments using baited artificial nests which have shown a positive correlation between egg depredation and proximity to the forest edge (Wilcove 1985, Andrén and Angelstam 1988, Berg et al. 1992). Most of these studies have been conducted in the north temperate zone, and only recently have scientists studied the effects of forest edges on nest predation in the tropics. Gibbs (1991) demonstrated an association between nest loss and type of forest edge, with elevated nest loss observed at forest/second-growth edges, but not at forest/pasture borders. He speculated that second-growth forest provides more cover and food resources for predators, thus higher levels of animal movement and nest loss may be expected. Most studies at all latitudes have focused on the forest/field ecotone produced through anthropogenic means (induced edges, sensu Yahner 1988), and only a few studies relate patterns of egg predation to quantitative measures of vegetation structure (e.g., Kelly 1993, Seitz and Zegers 1993, Thurber et al. 1994). Natural disturbances, however, such as blowdowns, tree-falls, and fire, may also produce forest edges (inherent edges, sensu Yahner 1988), resulting in forest fragmentation and regeneration with a mosaic quality. In the Caribbean, hurricanes are a major factor in shaping forest vegetation structure, often resulting in patchy damage that affects forest stand structure and dynamics for decades (Brokaw and Grear 1991, Brokaw and Walker 1991).

In this study we used artificial nests (cf Wilcove 1985) to examine nest predation in subtropical wet, and lower montane wet forest in Puerto Rico. Our purpose was to assess patterns of nest predation across a hurricane damaged forest landscape. We compared loss of ground and elevated nests in forest edge habitats to that in forest interior sites at a range of distances from the induced forest edge. Additionally, we quantified forest vegetation and structure at 59 forest interior nest sites and related patterns of nest predation to these variables.

STUDY AREA AND METHODS

Field work was conducted during the songbird nesting season from 29 April–26 May 1993 in the Luquillo Experimental Forest (LEF, also known as Caribbean National Forest), Puerto Rico. The LEF encompasses 11,500 ha and includes four major vegetation associations (Ewel and Whitmore 1973) that are altitudinally stratified. These are the tabonuco, or subtropical wet forest (200–600 m), palo colorado, or lower montane wet forest (600–900 m), palm forest or brake (>600 m), and the cloud forest (>850 m) (Brown et al. 1983). Portions of the forest were damaged by Hurricane Hugo in September 1989 (Walker et al. 1991).

In most trials we used straw-colored wicker (split bamboo), open-cup nests measuring 100 mm (diameter) by 60 mm (depth) obtained from pet supply stores. Predation rates have been shown to vary with differences in artificial nest appearance (Martin 1987) and with 'real' nests (i.e., unmanipulated nests built by and attended by birds) (Martin 1987, Willebrand and Marcström 1988). Therefore, we compared predation levels between artificial

nests and 'natural' nests. Our natural nests were fashioned from abandoned Bananaquit (*Coereba flaveola*) nests. Although these are typically domed nests, they were easily rearranged into a cup-shaped nest

In all experiments nests were baited with two fresh Japanese quail (*Coturnix coturnix*) eggs (cf Wilcove 1985). We placed nests at the base of trees with the cup nested in the ground (ground nests), and 1.5–2.0 m above the ground in trees or saplings (elevated nests). Elevated nests generally were wedged in forked or trifurcated branches, 0.5–1.0 m from the tree trunk, and sometimes were stabilized with a light gauge wire hanger assembly provided with the nest. Highly exposed nest sites were avoided but no other measures were utilized to conceal the nests or eggs. In all trials forest edge was defined by a paved, two lane highway with 5–10 m wide mowed shoulders. To minimize possible phenological influences, all nests within each trial were placed on the same day or on two consecutive days. Nests were checked in an initial trial every other day for signs of predation until at least 50% of all nests had been depredated. A nest was considered depredated if one or both eggs were found broken or missing. We used these results to redefine our protocol so that in later trials we only visited the nest sites once at the conclusion of the trial. In these trials nests were considered successful if both eggs survived to day six.

The manner of egg depredation was noted as evidence of a predator's identity. Potential nest predators included the exotic species, domestic dog, feral cat, Indian mongoose (*Herpestes auropunctatus*), and black rat (*Rattus rattus*), and the native Pearly-eyed Thrasher (*Margarops fuscatus*), Puerto Rican boa (*Epicrates inornatus*), and the land crab (*Epilobocera sinuatifrons*).

We conducted three sets of experiments. We tested the null hypothesis that there is no difference between predation rates on artificial and natural nests. Twelve elevated nests of each nest type were baited and placed at alternate stations at 50 m intervals along a transect 25 m from and parallel to the forest edge. All nests were placed in tabonuco forest. After six days the number of depredated nests of each type was recorded. A second trial tested the hypotheses that nest success decreases near induced forest edges, and that ground nests are depredated at a higher rate than elevated nests. We set ten transects perpendicular to the induced forest edge in the tabonuco forest (270–560 m). Along each transect six distances were marked at 5 m, 25 m, 50 m, 100 m, 150 m, and 250 m. At each of these stations, two baited, artificial nests were placed (one elevated and one ground) at least 10 m apart. After six days the nests were revisited and signs of depredation recorded. Finally we tested the hypothesis that nest patch (sensu Kelly 1993) vegetation characteristics are correlated with predation rates. Fifty-nine stations were located along four transects which traversed a mosaic of hurricane damaged and relatively undamaged tabonuco and palo colorado forest. In all cases nest sites were located 30 m from a narrow foot trail, 200 m from the next nearest nest site, and a minimum of 250 m from the nearest induced forest edge. At each station we placed two artificial nests (one elevated and one ground) at least 10 m apart. After six days the nests were revisited and signs of depredation recorded.

Nest patch characteristics were estimated within a radius of 11.1 m (0.04 ha) of the nest site, with sampling transects extending in cardinal compass directions from the nest site to the perimeter of the patch. At each plot the following characteristics of the vegetation structure were quantified: (1) Canopy cover was estimated at five points at 1.6 m intervals along the north, south, east and west radii of the circular plot. An ocular tube was used to record the percentage of green vegetation in the canopy at each point (sensu Winkworth and Goodall 1962) and then the mean canopy cover present at these 20 points was calculated. (2) Canopy height was calculated as the mean of the heights of the ten tallest trees in the nest patch as measured with a rangefinder. (3) Maximum canopy height was similarly measured as the height of the tallest tree in the plot. (4) Shrub density was measured as the

TABLE 1
VEGETATION VARIABLES (AND THE CODE USED TO DESCRIBE THEM) USED IN NEST PATCH ANALYSES

Variable code	Variable description
TREE1	Number of trees 3–8 cm dbh
TREE2	Number of trees 8–15 cm dbh
TREE3	Number of trees 15–23 cm dbh
TREE4	Number of trees 23–38 cm dbh
TREE5	Number of trees >38 cm dbh
CANHT	Mean canopy height
MAXHT	Maximum canopy height
SHRUB	Number of woody and herbaceous stems <3.0 cm dbh
COVER	Mean canopy cover
FHC00	Foliage height class 0–0.5 m
FHC01	Foliage height class 0.5–1.0 m
FHC02	Foliage height class 1.0–1.5 m
FHC03	Foliage height class 1.5–2.0 m
FHC04	Foliage height class 2.0–2.5 m
FHC05	Foliage height class 2.5–3.0 m
FHC06	Foliage height class 3.0–4.0 m
FHC07	Foliage height class 4.0–6.0 m
FHC08	Foliage height class 6.0–8.0 m
FHC09	Foliage height class 8.0–10.0 m
FHC10	Foliage height class 10.0–12.0 m
FHC11	Foliage height class 12.0–15.0 m
FHC12	Foliage height class 15.0–20.0 m
CECRO	Percent of total stems identified as *Cecropia*
TIPUP	Percent of total stems with exposed root wads (tip-ups)
DEAD	Percent of total stems which are dead

number of woody or herbaceous stems <3.0 cm dbh (diameter at breast height) present within 1 m of each transect. (5) All trees >3.0 cm dbh in the nest patch were counted and placed into one of five size classes. Size classes were 3–8 cm, 8–15 cm, 15–23 cm, 23–38 cm, and >38 cm. (6) A foliage height profile was determined for each nest patch by recording the presence of vegetation touches on a tube raised vertically 3.0 m into the canopy. Touches beyond 3.0 m were estimated. Measurements were taken at five points at 1.6 m intervals along each of the four cardinal radii (20 points total). The presence of touches was recorded at height classes: 0–0.5 m, 0.5–1.0 m, 1.0–1.5 m, 1.5–2.0 m, 2.0–2.5 m, 2.5–3.0 m, 3.0–4.0 m, 4.0–6.0 m, 6.0–8.0 m, 8.0–10.0 m, 10.0–12.0 m, 12.0–15.0 m, and 15.0–20.0 m. (7) The number of *Cecropia shreberiana* stems were counted and expressed as a percentage of the total stems in the plot ([Cecropia stems/total stems] × 100). (8) Exposed root wads or "tip-ups" were counted and recorded as a percentage of the total stems. (9) Finally, we calculated the percentage of trees that were dead (vertical or horizontal, >3.0 cm dbh). These vegetation variables and the codes used to describe them are summarized in Table 1.

We used the software package SYSTAT Version 5.2 (Wilkinson 1992) in all statistical analyses. Where data were not normally distributed non-parametric statistics were used.

Except where otherwise stated, a probability of Type 1 error of 0.05 or less was accepted as significant but we show greater values for descriptive purposes.

We tested whether nest success was independent of nest type (artificial or natural), or nest location (ground or elevated) by analyzing depredation levels in a 2 × 2 contingency table using Yates' correction of a G-test of independence which corrects for small samples (Sokal and Rohlf 1994). The influence of distance from the induced edge on nest success was analyzed in a R × C test of independence with a *G*-statistic (Sokal and Rohlf 1994) with results for ground and elevated nests analysed separately. In both cases results from nests placed at each distance (5 m, 25 m, 50 m, 100 m, 150 m, 250 m) were first tested separately. We were unable to reject the null hypothesis of independence between nest success and distance from the edge, so we then pooled observations at 5–50 m and 100–250 m in order to increase the number of observations per cell. This was justified by Paton's (1994) observation that the most conclusive studies suggest that edge effects usually occur within 50 m of an edge. We then used a *G*-test of independence with Yates' correction for continuity to test whether nest success was independent of distance from edge.

Signs suggesting method of egg loss were recorded from 42 depredated ground nests and 24 depredated elevated nests at forest interior nest sites. Observations were placed into one of four categories: (1) eggs removed and nest disturbed; (2) eggs removed but nest remains intact; (3) shell fragments remain in intact nest; or (4) rat signs (teeth marks or feces) present. We used a R × C test of independence to test the null hypothesis that there was no difference in types of egg depredation between ground and elevated nests.

In the final trial nest success was correlated with vegetation characteristics surrounding nest sites in interior forest. Ground and elevated nests were again analyzed separately. Pearson product-moment correlation coefficients were calculated for all pairwise comparisons of vegetation variables. We then eliminated from subsequent analyses three variables which were found to be highly correlated ($r > 0.70$) with other measures of vegetation structure: maximum canopy height (correlated with mean canopy height), foliage height class 2.0–2.5 m (correlated with foliage height classes 1.5–2.0 m and 2.5–3.0 m), and foliage height class 12–15 m (correlated with foliage height classes 10–12 m and 15–20 m) were eliminated.

Each remaining vegetation variable was then analyzed using an independent samples *t*-test (separate variances) with a Bonferroni correction for multiple comparisons to test the equality of the means of each vegetation variable grouped by nest success (depredated or non-depredated). In some cases where the assumption of normality was violated, a Mann-Whitney *U*-test was also utilized, but in all such cases the results were comparable. Only results from *t*-tests are reported here as the test is considered robust. Vegetation variables that did not differ significantly ($P > 0.10$) between depredated and non-depredated sites were then eliminated from further analyses.

Multivariate analysis of the six remaining vegetation variables associated with elevated nest success, and the two remaining vegetation variables associated with ground nest success, was performed to determine the relative contribution of each variable. We used a discriminate function analysis (Morrison 1976) to compare the vegetation characteristics surrounding depredated and non-depredated nests. The discriminate function analysis calculates a linear combination of the vegetation variables such that the difference between depredated and non-depredated sites is as large as possible. The linear discriminate function is: $z = \alpha_1 x_1 + \alpha_2 x_2 + \ldots, + \alpha_P x_P$, where z is the discriminant score for P vegetation variables normalized with a mean of 0 and a standard deviation of 1, α is the weight for the vegetation variable i, and x is the value of vegetation variable i ($i = 1, \ldots, P$). The Wilks' Lambda *F*-statistic was used to test the equality of discriminant scores ($P > 0.10$).

TABLE 2

PERCENTAGE OF GROUND AND ELEVATED NESTS DEPREDATED AT EACH OF SIX DISTANCES FROM THE FOREST EDGE

	Distance from forest edge (m)					
	5[a]	25[a]	50[a]	100[b]	150[b]	250[b]
Ground nests[c]	90%	90%	80%	90%	78%	89%
Elevated nests[c]	50%	50%	70%	60%	44%	56%

[a] Treatment contained ten nests.
[b] Treatment contained nine nests.
[c] Percentage of artificial nests in which one or both eggs were removed or damaged after six days of exposure.

RESULTS

We found that more natural nests than artificial nests were preyed upon ($\chi^2 = 6.042$, df = 1, $P = 0.014$). After six days of exposure, eggs in nine of 12 natural nests were depredated while eggs in two of 12 artificial nests were lost. Utilizing artificial nests, levels of depredation were significantly higher ($\chi^2 = 12.024$, df = 1, $P = 0.0005$) for ground nests (86% depredated, N = 58) than for elevated nests (55% depredated, N = 58). But we found no difference in levels of depredation between the edge (5–50 m) and the forest interior (100–250 m; Table 2) for either ground nests or elevated nests (both $\chi^2 = 0.000$, df = 1, $P = 1.000$).

After six days of exposure 42 of 59 ground nests and 23 of 59 elevated nests were depredated in forest interior sites. Depredation of ground nests (Table 3) occurred where there was significantly higher shrub density, and a suggestion ($P < 0.10$) of more vegetation in the 2.5–3.0 m foliage height class. Depredation of elevated nests (Table 4) occurred where there was significantly less canopy cover, significantly more vegetation in the 0–0.5 m and 0.5–1.0 m foliage height classes, significantly less vegetation in the 3.0–4.0 m height class, and a significantly lower percentage of *Cecropia* trees in the nest patch. Among elevated nests which were depredated there was also a suggestion ($P < 0.10$) of more vegetation in the 1.0–1.5 m foliage height class.

Fisher's linear discriminant function equation for ground nests is: z = 0.0156(SHRUB) + 0.0580(FHC05) − 1.5854. Normalized scores produced using the means of depredated and non-depredated nests were 0.2148 and −0.2075 respectively. We used the Wilks' Lambda *F*-statistic to reject the equality of these discriminant scores ($P = 0.091$). Using this model, counts of shrubs and foliage density in the 2.5–3.0 m height class, successfully distinguished 59% of the sites with depredated and non-depredated ground nests in the forest interior.

Fisher's linear discriminant function equation for elevated nests is: z =

TABLE 3

COMPARISON OF MEAN (STANDARD ERROR) VALUES OF VEGETATION PARAMETERS SURROUNDING DEPREDATED AND NON-DEPREDATED GROUND NESTS

Vegetation variable[a]	Depredated	Non-depredated	P^b
TREE1	39.38 (2.90)	32.18 (3.32)	0.110
TREE2	10.69 (0.94)	84.7 (1.16)	0.706
TREE3	15.31 (1.04)	14.35 (2.27)	0.145
TREE4	4.48 (0.44)	3.59 (0.55)	0.214
TREE5	2.33 (0.32)	2.18 (0.45)	0.778
CANHT	10.24 (0.36)	10.43 (0.85)	0.838
SHRUB	95.83 (5.72)	73.23 (7.89)	0.027
COVER	86.31 (2.04)	84.41 (5.03)	0.730
FHC00	16.00 (0.46)	16.47 (0.68)	0.572
FHC01	9.26 (0.57)	9.76 (1.42)	0.746
FHC02	7.31 (0.47)	6.71 (1.21)	0.646
FHC03	5.45 (0.53)	6.23 (1.03)	0.507
FHC05	5.26 (0.50)	4.06 (0.50)	0.095
FHC06	9.00 (0.72)	9.12 (1.03)	0.926
FHC07	6.21 (0.52)	5.00 (0.85)	0.232
FHC08	7.00 (0.67)	6.53 (0.95)	0.689
FHC09	5.69 (0.73)	8.18 (1.39)	0.126
FHC10	4.07 (0.72)	5.94 (0.94)	0.122
FHC12	0.40 (0.22)	0.88 (0.45)	0.351
CECRO	6.67 (1.79)	7.53 (2.69)	0.791
TIPUP	0.67 (0.21)	0.53 (0.26)	0.686
DEAD	8.20 (0.74)	6.87 (1.22)	0.361

[a] Vegetation variables described in Table 1.

[b] *P*-values from independent samples *t*-tests (separate variances) with a Bonferroni correction for multiple comparisons based on 59 forest-interior nests.

-0.0127(COVER) + 0.0116(FHC00) + 0.1194(FHC01) + 0.0868(FHC02) $-$ 0.0946(FHC06) $-$ 7.1382(CECRO) + 0.3434. Normalized scores produced using the means of depredated and non-depredated nests were 0.7364 and -0.0974 respectively. We rejected the equality of these scores using the Wilks' Lambda test statistic ($P = 0.010$). Using this model, success of forest interior elevated nests was correctly classified by these six vegetation variables in 71% of cases.

The absolute value of the linear correlation of each vegetation variable with the discriminant function was calculated for ground nests (SHRUB, $r = 0.97$; FHC05, $r = 0.62$) and for elevated nests (COVER, $r = 0.52$; FHC00, $r = 0.43$; FHC01, $r = 0.64$; FHC02, $r = 0.42$; FHC06, $r = 0.47$; CECRO, $r = 0.60$). These correlations are a relative indication of the strength of the specific vegetation variable to discriminate between depredated and non-depredated nests in the discriminant function equation.

TABLE 4
COMPARISON OF MEAN (STANDARD ERROR) VALUES OF VEGETATION PARAMETERS SURROUNDING DEPREDATED AND NON-DEPREDATED ELEVATED NESTS

Vegetation variable[a]	Depredated	Non-depredated	P^b
TREE1	32.70 (3.61)	40.25 (2.92)	0.110
TREE2	13.74 (1.75)	15.86 (1.15)	0.318
TREE3	8.91 (1.07)	10.78 (1.02)	0.213
TREE4	4.00 (0.53)	4.36 (0.47)	0.611
TREE5	2.52 (0.44)	2.14 (0.33)	0.491
CANHT	9.80 (0.46)	10.62 (0.49)	0.232
SHRUB	86.04 (6.06)	91.42 (6.93)	0.562
COVER	80.00 (4.40)	89.44 (1.57)	0.053
FHC00	17.04 (0.54)	15.55 (0.50)	0.050
FHC01	11.35 (0.95)	8.17 (0.63)	0.008
FHC02	8.26 (0.75)	6.42 (0.59)	0.060
FHC03	6.09 (0.78)	5.42 (0.61)	0.501
FHC05	4.78 (0.75)	5.00 (0.43)	0.803
FHC06	7.52 (0.91)	10.00 (0.72)	0.039
FHC07	5.87 (0.76)	5.86 (0.55)	0.993
FHC08	6.83 (0.86)	6.89 (0.72)	0.956
FHC09	6.39 (0.96)	6.42 (0.91)	0.985
FHC10	4.39 (0.95)	4.75 (0.75)	0.769
FHC12	0.78 (0.40)	0.39 (0.21)	0.388
CECRO	2.09 (1.16)	10.00 (2.17)	0.002
TIPUP	0.87 (0.26)	0.47 (0.22)	0.251
DEAD	6.97 (0.80)	8.35 (0.90)	0.260

[a] Vegetation variables described in Table 1.
[b] *P*-values from independent samples *t*-tests (separate variances) with a Bonferroni correction for multiple comparisons based on 59 forest-interior nests.

Ground and elevated nests showed different patterns of depredation ($\chi^2 = 17.981$, df = 3, $P = 0.001$). Eggs disappeared in 67% of the depredated ground nests (N = 42) and in 42% of the depredated elevated nests (N = 24). Shell fragments were found in 19% of depredated ground nests (N = 42), and in 42% of depredated elevated nests (N = 24). Two percent of ground nests (N = 42) showed signs of rat presence, as did 8% of the elevated nests (N = 24). Displacement or nest destruction was found in 12% of the depredated ground nests (N = 42) and 8% of the depredated elevated nests (N = 24).

DISCUSSION

In studies in the northern temperate zone, Martin (1987) has shown a poor correlation between predation rates on artificial and natural nests and warned against overgeneralizing results based on artificial nest studies

alone. Our results show higher predation on natural nests, the first reported from a tropical forest, indicating that the levels of predation we recorded on artificial nests may underestimate actual predation levels. These data suggest that the proportion of nests lost cannot be translated to actual predation rates on 'real' nests, and should be used only as a means of answering comparative questions of rates of predation in different habitats (Seitz and Zegers 1993) and under different conditions.

We found ground nests to have higher rates of depredation than elevated nests, and this is consistent with many previous studies in a variety of habitats (Loiselle and Hoppes 1983; Wilcove 1985; Yahner and Scott 1988; but see Martin 1992a, b; Seitz and Zegers 1993). This difference is likely the result of the relative abundance and influence of terrestrial, mammalian predators as opposed to avian or mammalian arboreal predators, and the influence of habitat and vegetation characteristics in concealing predators or nests (see below).

The absence of a relation between nest predation and distance from a road was unexpected for several reasons. First, roads have been used in previous studies to define edges (Boag et al. 1984) and have negatively affected nest success (Yahner 1988). Second, many ecological effects of roads have been noted, including their use as corridors by predatory corvids (Angelstam 1986), and by dogs, cats, and Pearly-eyed Thrashers in the LEF (J. Wunderle, pers. obs.), and an increase in edge-related passerines (Wunderle et al. 1987). Furthermore, roads frequently increase the incidence of landslides, contributing to the availability of disturbed sites which may serve as stepping stones or corridors for invasion of the forest by exotic species.

A likely explanation for our failure to find a positive relationship between nest success and distance from the forest edge is that predatory edge specialists are responding not only to the induced forest edge (the road) but to inherent forest edges and the natural heterogeneity in vegetation throughout this tropical forest. We suggest that our results reflect a continuing effect of Hurricane Hugo on nest predation 3½ years after the passage of the storm.

The passage of Hurricane Hugo resulted in a radical change in the physical structure of the forest (Brokaw and Walker 1991) resulting from defoliation and the uprooting and snapping of tree trunks. But the extent of localized damage was affected by topography, stand characteristics, and the properties of individual trees and species (Brokaw and Grear 1991), resulting in a patchwork of damage. Following the hurricane, differential recovery, recruitment, and growth rates contributed to a forest structure in which the disparate damage is expected to be evident for decades (Brokaw and Walker 1991). At present, damaged forest is char-

acterized by a more open canopy, the creation of early successional vegetative associations (Brokaw and Walker 1991, Tanner et al. 1991), and the presence of *Cecropia shreberiana* in approximately ¼–⅓ of the created openings (D. J. Lodge, unpubl. data).

Our results suggest that egg predation occurred most frequently at both ground and elevated nests in areas damaged by the hurricane, but that differences in the recovery of vegetation also affected the probability of nest success. Among our direct measures of damage (canopy cover, tip-ups, dead stems), only canopy cover was found to differ significantly between depredated and non-depredated, ground or elevated nests. The absence of a relationship of tip-ups or dead stems with depredation may reflect the variety of mortality factors at play in the forest in the years since the hurricane, or this hurricane damage may have been obscured in the recovery process. Changes in canopy closure would be expected to change much less rapidly. Much stronger relationships with nest success were seen in measures of forest recovery, represented by the prevalence of early successional vegetative associations (shrubs; foliage height classes 0–0.5 m, 0.5–1.0 m, 1.0–1.5 m) that respond positively to canopy openings. Another indicator of recovery, *Cecropia* stems, may have obscured some of these vegetative effects because of its patchy distribution, and its ability to shade out the recovery response of some understory species.

Among ground nests we found a positive relationship between shrub density and egg predation and this vegetation variable was very highly correlated with our discriminant function equation. This suggests that predation on ground nests was higher in forest patches where hurricane recovery may be present. Foliage in the 2.5–3.0 m range was only weakly associated ($P < 0.10$) with predation of ground nests and was moderately correlated with the discriminant function. We therefore consider it of minor importance in distinguishing between successful and unsuccessful nest sites.

Among elevated nests, egg predation was associated with nest sites having a more open canopy, and a suite of vegetation characteristics indicating a dense understory. A consistent trend is evident where the lower foliage height classes (0–0.5 m, 0.5–1.0 m, 1.0–1.5 m) are positively related to egg predation, while the mean score for the higher foliage variables (canopy cover, foliage height class 3.0–4.0 m) are negatively associated with egg loss. These data are consistent with the possibility that predation is higher in some areas heavily affected by the hurricane, but where colonization by *Cecropia* has not occured. Sites with an abundance of *Cecropia* had lower rates of nest predation than sites with few or no *Cecropia*. Although *Cecropia* responds to disturbance and would

seem to favor nest predators, we suspect that predators avoid the branchless *Cecropia* and its typically open understory (Martin 1993, Kelly 1993).

We can only speculate on the identities of egg predators. Based on our observations of the modes of predation, we believe that most of the elevated nests were depredated by our only abundant avian predator, the Pearly-eyed Thrasher. The thrasher is known to be a very important source of mortality of eggs of many bird species (Snyder et al. 1987), and commonly breaks the eggs, leaving large jagged fragments in the nest (W. Arendt, pers. comm.). Such fragments were found in 19% of ground nests, but in more than 40% of elevated nests, that were depredated.

Eggs were carried away from most depredated ground nests, as well as many elevated nests. Predators large enough to remove eggs include the Puerto Rico boa, though it is most commonly seen at elevations below 400 m (Snyder et al. 1987), dogs, cats, rats, and the mongoose. Because mongooses are numerous and widespread, we believe that they may be responsible for much of the ground nest depredation, but more data are needed.

We compared predation rates on artificial, open cup nests from this study to those reported from three other tropical, forest-interior sites. Because exposure periods differed, we calculated a daily predation rate, assuming that predation pressure is constant over the duration of each study. Gibbs (1991) reported predation rates of mainland Costa Rican ground nests (3.4%) and elevated nests (1.4%) quite similar to those reported by Loiselle and Hoppes (1983) from their Panamanian mainland site (3.0% for both ground and elevated nests). In contrast, we observed much higher daily predation rates for both ground nests (11.8%) and elevated nests (6.5%) in this insular subtropical forest, as did Loiselle and Hoppes (1983) on Barro Colorado Island (BCI, Panama) (50.0% and 9.5% respectively). As Loiselle and Hoppes (1983) noted, the magnitude of the difference in predation rates between BCI and the mainland is remarkable. Karr (1982) and Gibbs (1991) have suggested that predation at BCI may be unusually high due to an elevated density of nest predators on the recently created (1914) island. Predation rates from this Puerto Rican forest, however, approach those from BCI (particularly for elevated nests) and suggest that the high predation rates from BCI may not be an anomaly from a unique island, but characteristic of insular forest habitats. While the diversity of predators is undoubtably lower in island habitats, we suspect that the density of predators may be much higher. Potential predators such as thrashers, rats, and mongooses are all extremely abundant. Caribbean islands are also more prone to disturbance (such as hur-

ricanes; Walker et al. 1991), thus creating habitat that is frequently utilized by these same nest predators.

The many effects of hurricanes on birds are well known (reviewed in Wiley and Wunderle 1994), as is the short-term response of bird populations to hurricane damage (Wiley and Wunderle 1994). We present evidence for long-term, increased predation associated with hurricane-induced early successional vegetative associations. The fact that we were unable to identify an induced edge effect may be attributed to the creation of canopy openings and a matrix of inherent edge habitat across the forest (habitat frequently used by nest predators) following the passage of Hurricane Hugo.

ACKNOWLEDGMENTS

M. A. de la Fuente, C. Laboy, A. Ortiz, T. Ruszkowski, and M. Sugden, provided help in quantifying vegetation structure. W. Arendt, D. J. Lodge, J. M. Meyers, and B. R. Parresol provided advice with statistics and data interpretation. W. Arendt, A. Lugo, J. M. Meyers, H. A. Raffaele, and an anonymous reviewer provided constructive comments on the manuscript.

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Wilson Bull., 107(4), 1995, pp. 603–614

LANDSCAPE CHARACTERISTICS ASSOCIATED WITH ACTIVE AND ABANDONED RED-COCKADED WOODPECKER CLUSTERS IN EAST TEXAS

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ABSTRACT.—I investigated spatial characteristics of Red-cockaded Woodpecker (*Picoides borealis*) cluster sites in the Raven Ranger District of the Sam Houston National Forest, Texas. Active cluster sites were larger and closer to other active clusters than inactive ones and had larger gravity interaction values. Inactive sites were significantly more isolated than were active clusters, they were more likely to be surrounded by inimical land uses, and they were less likely to be connected by corridors of mature timber to active cluster sites. This research indicates that spatial landscape parameters influence Red-cockaded Woodpecker cluster status and they should be considered in management plans for the species. *Received 24 Oct. 1994, accepted 16 May 1995.*

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperative breeder with highly specific habitat requirements. Nesting and roosting cavities are excavated in living pine trees that are typically infected with heart-rot fungus (*Phellinus pini*) and that tend to be the older trees in a forest (Jackson 1977, Conner and Locke 1982, Hooper 1988, Hooper et al. 1991b, Conner et al. 1994). Cavity trees occur in clusters, and the woodpeckers are intolerant of hardwood midstory development in the cluster sites (Loeb et al. 1992, Kelly et al. 1993). Red-cockaded Woodpeckers have declined throughout their range because of a shortage of potential cavity trees (Hooper 1988) and infrequent fire regimes to control midstory development (Conner and Rudolph 1989). Where these problems are absent, populations have been stable or have increased (Hooper et al. 1991a, USFS 1993, Conner et al. 1995). In three of the National Forests in Texas, the Angelina, Davy Crockett, and Sabine, past declines had been precipitous, amounting to a decrease in active clusters of 10% per year between 1983 and 1988 (Conner and Rudolph 1989). However, populations in all National Forests in Texas have stabilized or increased in recent years (Conner et al. 1995). The timber characteristics required for a forest stand to be used by Red-cockaded Woodpeckers are known (Boone 1980, Hooper et al. 1980, USFWS 1985, Walters 1991), but landscape requirements of usable patches have been studied little. Conservation of species requires that adequate areas of habitat are maintained, with the size and configuration of "adequate" habitat differing from spe-

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cies to species and from situation to situation. Bird species richness and abundance may be related more to landscape structure than to habitat physiognomy (McCollin 1993), and birds with restrictive habitat structure needs, such as Kirtland's Warbler (*Dendroica kirtlandii*) and the Northern Spotted Owl (*Strix occidentalis caurina*), are also dependent on patch size and configuration (Jakubauskas 1992, Lamberson et al. 1992). To maintain biodiversity, whether in the general sense or the case of an individual species, requires a landscape approach (Harris 1984, Hansson and Angelstam 1991, Franklin 1993).

The U.S. Forest Service (USFS) is managing southern pine forests to improve and maintain Red-cockaded Woodpecker habitat (USFS 1985, Hooper et al. 1990, Walters 1991, USFS 1991), primarily by thinning, midstory reduction, and prescribed burns (Conner 1989, Conner and Rudolph 1991b, Conner et al. 1995) in active cluster sites and by creation of replacement and recruitment stands of suitable habitat. Management on all National Forests in Texas during the past three years has included the use of artificial cavity inserts and translocation of woodpeckers to increase the number of breeding pairs in each forest (Conner et al. 1995).

Dispersal of birds into new territories seems to be a limiting factor on populations: Ligon et al. (1986) reported that establishment of new clusters was virtually unknown. More recently, it has been demonstrated that populations can expand when suitable habitat is present (Hooper et al. 1991a). In addition, Copeyon et al. (1991) and Walters et al. (1992) have demonstrated the success of new cluster formation when artificial cavities were provided. This emphasizes the need for preservation of existing habitat and creation of new habitat by management. Furthermore, particularly in the absence of translocation, individuals must be able to disperse from existing clusters into suitable habitat: connectivity among existing patches, and between existing and newly-created patches, must be adequate (Ligon et al. 1986). The objectives of this study were to determine whether landscape characteristics, particularly measures of isolation, were different between active and inactive Red-cockaded Woodpecker cluster sites and how to use knowledge of any differences in habitat management.

METHODS

The study area comprised Compartments 1 through 54 of the Raven Ranger District of the Sam Houston National Forest (SHNF), Texas (Fig. 1). The SHNF is 80 km north of Houston, in the area known as the Pineywoods. It covers an area of 193,622 ha, of which 65,217 ha are National Forest lands; the remainder are private inholdings which were not considered for this study.

The primary source of data for this study was the USFS stand-map database for the Raven District. Line data of the district stand maps were imported to ARC/INFO, version 5.1 (Environmental Systems Research Institute 1989). The line data, which were in preliminary

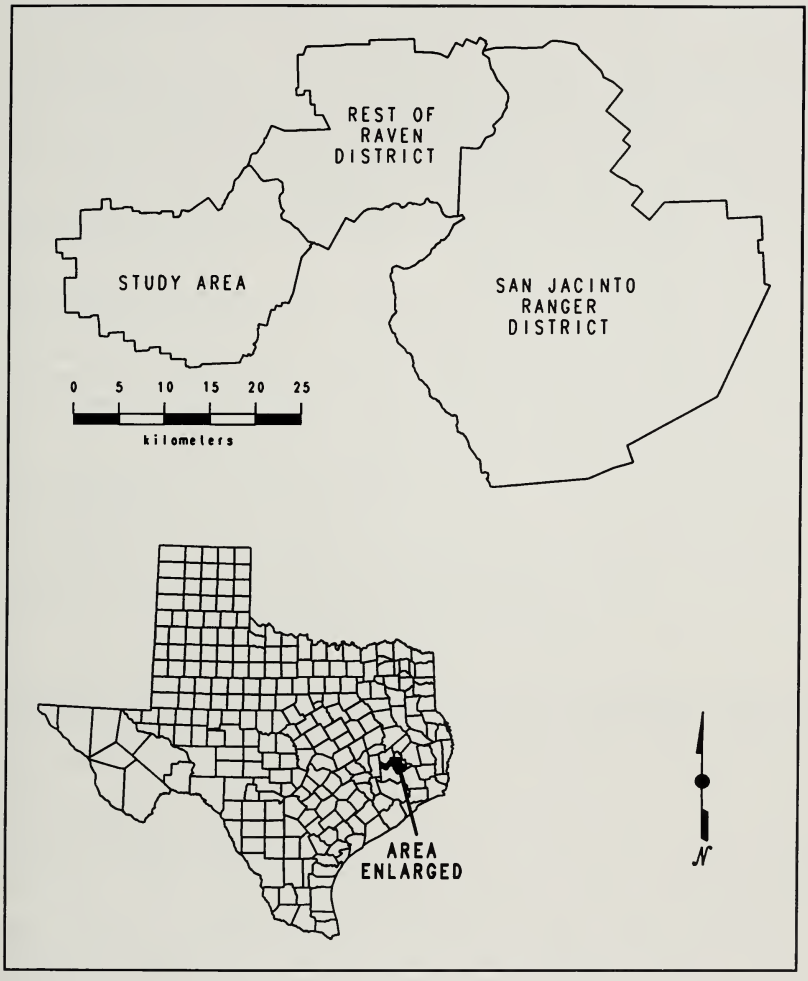

FIG. 1. Study area location map, Raven Ranger District, Sam Houston National Forest, Texas.

form, were compared to the hard-copy stand maps obtained from the Raven District, and errors were corrected using a visual display terminal. Attribute data on the stands were read from the USFS Continuous Inventory of Stand Conditions-II (CISCII) computerized database and attached to the appropriate stand polygons.

Many polygons were drawn on the stand maps, and subsequently digitized, that corresponded either to cut areas in stands of mature trees (inclusions) or stands of relict trees in young plantations. The nature of the inclusions and relict stands was ascertained by visually interpreting stereopairs of 1:24,000 false-color infrared aerial photographs of the study area, taken in 1988 through 1991.

For statistical analyses of the data SAS-STAT version 6.07 (SAS Institute 1989) was

used. General comparisons of parameters between different active and inactive clusters were conducted with the Wilcoxon-Mann-Whitney signed-ranks test with tied-ranks correction and large-sample normal approximation with continuity correction (Wilcoxon test: Zar 1984). In each comparison, the null hypothesis was that there was no difference in parameter value between active and inactive cluster stands. A significance level of 0.05 was used.

The proximity of clusters to one another was assessed in three ways: as direct distance measurements, by a gravity model, and by determining the isolation coefficient for each cluster. The distance measurements were straight-line, edge-to-edge distances from each cluster, active or inactive, to the next nearest active cluster. The distances (DISTANCE) for active and inactive sites were compared.

The gravity model, derived from Newton's Law of Gravitation, is commonly used in urban geography (Hartshorn 1980), where population of a city is substituted for mass. Rudis and Ek (1981) applied the model to forest islands, and I substituted area of the cluster site for population. The model was also modified to use edge-to-edge distance, rather than center-to-center, since the woodpeckers are highly mobile within a cavity-tree cluster, and any deterrent to dispersal would be between the edge of one cluster and the edge of another. The gravity interaction (GRAVITY) between each cluster and the next nearest active cluster was calculated for all cluster sites, active and inactive, and the two classes were compared.

The isolation coefficient (II) of each cluster, a modification of the gravity model, is defined as follows (after Whitcomb et al. 1981): $II = 1 / \Sigma(A_i/d_i^2)$, where A_i = the area of each cluster site, i, within a given radius (d_o) from the study cluster, and d_i = the distance between cluster i and the study cluster. Three values of maximum distance (d_o) were investigated. The first was 4000 m (II4000), which exceeded the largest minimum centroid-to-centroid distance in the study area (ensuring that no stands would have an isolation coefficient of infinity) and approximated the known distance flown by individual birds reported by Boone (1980). The second maximum distance used was 1130 m (II1130), which corresponded to the effective radius of the largest home range of Red-cockaded Woodpeckers (400 ha) reported by Conner and Rudolph (1989). The third distance was 390 m, corresponding to the smallest home range (50 ha) that Conner and Rudolph (1989) listed. There are reports of birds covering greater distances (Hooper et al. 1980, Walters 1991), but these three values were the only ones considered here. For each of the three maximum distances, active cluster sites were compared to inactive ones; recruitment and replacement stands were compared to active cluster sites only in the 4000-m maximum distance case.

To determine the relationships between Red-cockaded Woodpecker clusters and surrounding landcover types, a neighbor analysis was performed. The percentage of cluster stand border shared with different landcover classes was compared for active and inactive sites. The neighboring landcover classes considered were sawtimber (ST), poletimber (PT), forest in regeneration (REG), seedling/sapling (SS), pasture (PAS), and open water (OW). A number of derived neighbor categories were created: ST + PT, ST + PT + REG, ST + PT + REG + SS, PAS + OW, and PAS + OW + SS.

To assess the impact of corridors on cluster status, the nature of the path from each cluster site to its next nearest active cluster was classified into one of four categories (1) direct (line-of-sight) path through pine sawtimber and/or poletimber; (2) indirect path through pine sawtimber and/or poletimber (deviation from line-of-sight to go around open country); (3) circuitous path that would require flying away from the target to stay within timber; and (4) no timber corridor adjacent to the cluster site (any area of land cover other than pine poletimber or sawtimber greater than 50 m wide completely surrounding the cluster). The frequencies of each class for active and inactive cluster sites were compared using a contingency-table log-likelihood test.

TABLE 1

SPATIAL STAND PARAMETERS IN ACTIVE AND INACTIVE CLUSTERS IN THE RAVEN RANGER DISTRICT, SAM HOUSTON NATIONAL FOREST, TEXAS

Parameter	Minimum		Maximum		Median		
	Active	Inactive	Active	Inactive	Active	Inactive	
Cluster site area, ha (AREA)	0.6	0.3	27.9	17.6	6.2	2.7	*
Distance from cluster site to nearest active cluster site, m (DISTANCE)	0	0	3320	3500	300	373	*
Gravity interaction between cluster site and nearest active cluster site (GRAVITY)	245	63	8×10^6	1×10^6	20×10^3	6×10^3	*
Isolation coefficient, d_2 = 4000 m (II4000)	0.4	0.5	119	45	2.1	3.8	*
Isolation coefficient, d_2 = 1130 m (II1130)	0.5	0.6	∞	∞	4.3	6.7	*

* Statistical significance between active and inactive cluster sites, Wilcoxon test, $\alpha = 0.05$.

RESULTS

The study site had a total area of 35,568 ha. Immature sawtimber covered 29% of the study area, followed by mature sawtimber with 25%. There were 107 active clusters with a total area of 699 ha, and 60 inactive clusters comprising 208 ha. All the active clusters and all but three of the inactive ones were in mature or immature sawtimber. There were 52 recruitment stands, managed to create attractive habitat for birds seeking new cluster sites, and 151 replacement stands, which are recruitment stands adjacent to existing active or inactive cluster sites. The dominant timber in the study area was loblolly pine, which covered 83% of the USFS lands. Shortleaf pine occupied another 9%, and hardwoods accounted for an additional 6%.

Active cluster stands were larger than cluster stands that had become inactive (Table 1; Wilcoxon test, $P = 0.0001$): median values were 6.2 ha compared to 2.7 ha. The distance from each active cluster to its next nearest active neighbor ranged from 0 m (in the case of contiguous clusters) to 3320 m (Table 1). The distance from each inactive site to the nearest active cluster had a similar range but somewhat higher median. The distributions of distances (Fig. 2) were significantly different, with inactive sites being further away from the closest active cluster than were active ones (Wilcoxon test, $P = 0.0151$). The majority of clusters, regardless of status, were close to their next nearest active cluster; 76% of

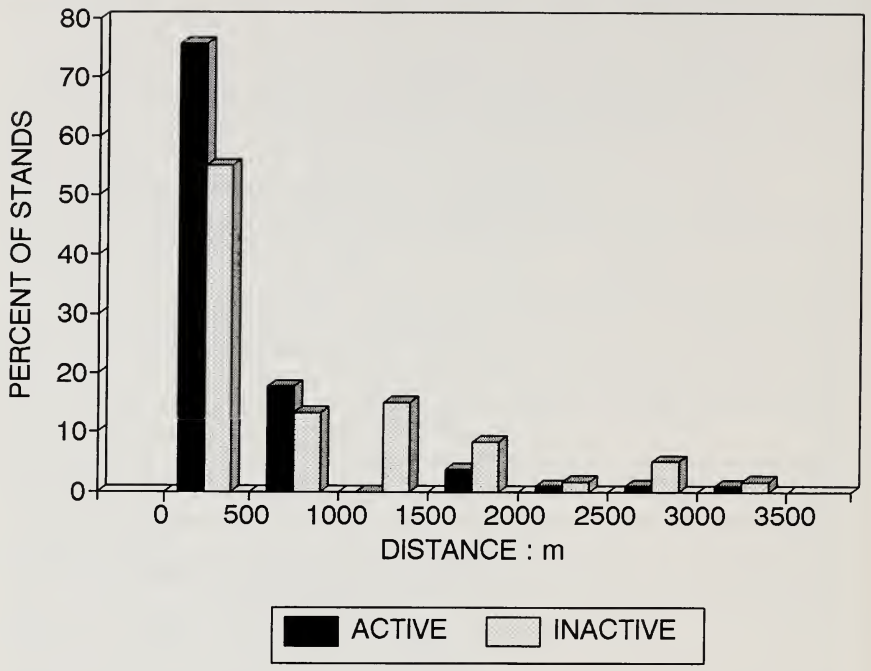

FIG. 2. Comparison of distance to nearest active cluster stand (DISTANCE) from active versus inactive clusters.

actives and 55% of inactives were within 500 m. However, 32% of inactive cluster sites were more than 1 km from the next nearest active cluster, compared to only 7% of active ones.

The gravity interactions between active clusters and their next nearest active neighbor had a much higher range and median than between inactive sites and their nearest active cluster (Table 1; Wilcoxon test $P = 0.0030$). While 62% of active clusters had gravity interactions greater than 10^4, only 42% of inactive cluster sites had values this high. Conversely, only 7% of active clusters had gravity interactions below 10^3, compared to 25% of inactive cluster sites (Fig. 3).

With a maximum search radius of 4000 m the isolation coefficients (II4000) of inactive sites were significantly higher than II4000 of active clusters (Table 1; Wilcoxon test, $P = 0.0207$). While 30% of inactive sites had II4000 values above eight, only 7% of active ones were this isolated (Fig. 4). Conversely, 82% of active sites were below four compared to 58% of inactive sites. Recruitment stand isolation coefficients (II4000) were significantly higher than active clusters (Wilcoxon test, *P*

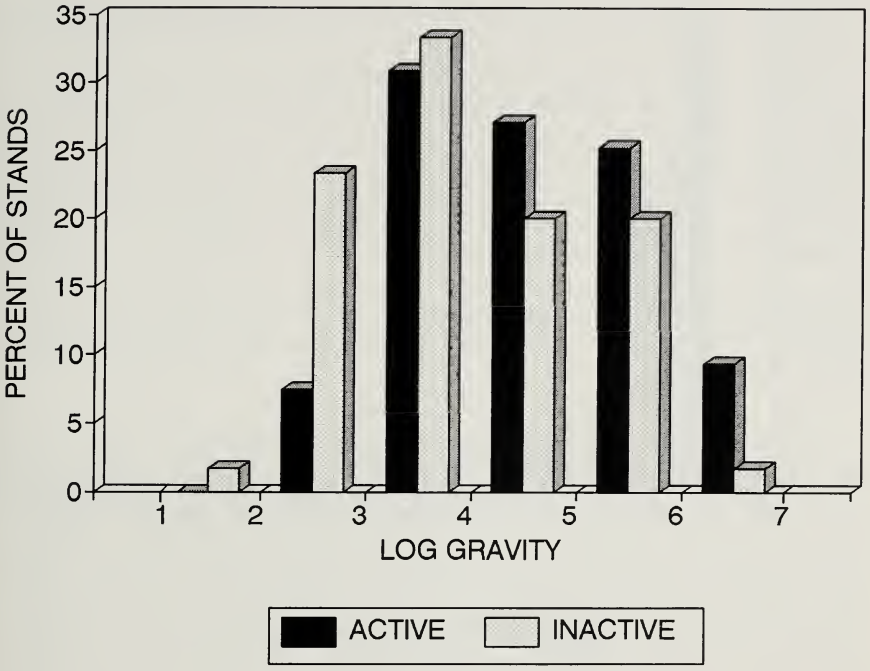

FIG. 3. Comparison of gravitational interaction with nearest active cluster stand (GRAVITY) for active versus inactive clusters. Note that the abscissa has a logarithmic scale.

= 0.0001). Replacement stand isolation coefficients, on the other hand, were significantly lower than active clusters (Wilcoxon test, $P = 0.0001$). When a maximum search radius of 1130 m was considered (Table 1), inactive sites still had significantly larger isolation coefficients (II1130) than did active clusters (Wilcoxon test, $P = 0.0234$). Nine of the active clusters (8%) had infinite isolation coefficients compared to 23 (38%) of the inactive ones. The maximum search radius of 390 m did not prove to be very instructive: only 14 of the active clusters (13%) and six of the inactive ones (10%) had finite isolation coefficients (II390).

There was no significant difference between active and inactive clusters in the percentage of cavity-tree cluster perimeter shared with any of the individual landcover classes or class groups except open country (PAS and PAS+OW). None of the active clusters shared their perimeter with pasture, compared to five of the inactive ones, a significant difference (Wilcoxon test, $P = 0.0016$). Three of the active clusters and six of the inactive ones shared part of their perimeters with the combined PAS+OW category (Wilcoxon test; $P = 0.0304$). Because there were only three active clusters and six inactive ones with any shared perimeter with

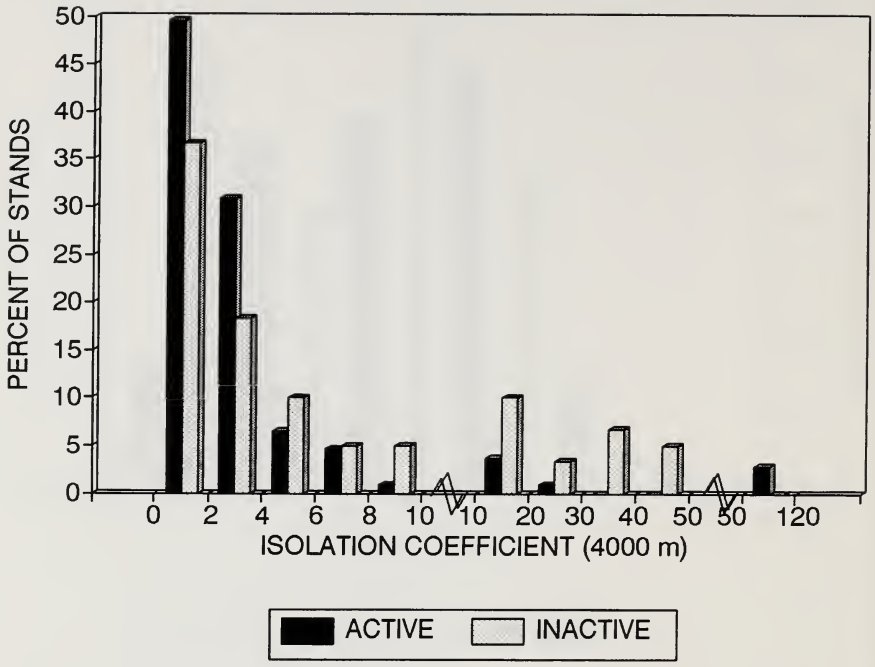

FIG. 4. Comparison of isolation coefficient, considering all active clusters within 4000 m (II4000), for active versus inactive clusters. Note the changes in abscissa scale at isolation coefficient values of 10 and 50.

PAS+OW, it was not possible to test the hypothesis that larger cluster stands could remain active in the face of inimical land uses around their perimeters than could smaller ones. For this analysis and the next, five inactive sites in young replanted stands (≤33 yr) were excluded.

There were direct corridors from 64% of the active clusters, compared to 67% of the inactive ones (Table 2). The primary difference between active and inactive cluster sites involved less-direct and absent corridors. Indirect or circuitous corridors formed a link to 34% of active clusters, compared to 18% of inactive ones, while corridors were absent around only 3% of active clusters versus 15% of inactive ones. A 4 × 2 contingency analysis of the data indicated that the frequency of different corridor classes was significantly different between active and inactive cluster sites (log-likelihood with small-sample adjustment $G = 10.11$, $0.01 \leq P \leq 0.025$).

DISCUSSION

Inactive cluster stands were smaller and more isolated from other woodpecker groups than were active cluster stands; all metrics for iso-

TABLE 2
NUMBER AND PERCENTAGE OF ACTIVE AND INACTIVE CLUSTERS WITH DIRECT, INDIRECT, CIRCUITOUS, AND ABSENT CORRIDORS

Cluster status	Corridor class				
	Direct	Indirect	Circuitous	Absent	Total
Active	68 (64)	26 (24)	10 (9)	3 (3)	107 (100)
Inactive	37 (67)	8 (15)	2 (4)	8 (15)	55 (100)
Total	105	34	12	11	162

Values in table are numbers (and percentages) of clusters of each status, active or inactive, in each corridor class. The differences were significant ($G = 10.11$, $0.01 \leq P \leq 0.025$).

lation, except II390, were significantly different between the two classes. In contrast, while Conner and Rudolph (1991a) found that forest fragmentation close to a cluster was associated with small group size, they found no difference in the number of active clusters within 2 km of a cluster between small and large groups. This indicates the value of using various different metrics to measure isolation. Gravity interaction and isolation coefficient, for example, which incorporate cluster area and distance between clusters, may give more insight into isolation than does the number of clusters within a given radius alone. Walters (1991) describes the population dynamics of cooperative breeders such as the Red-cockaded Woodpecker, and he points out that they are generally unsuccessful at long-range dispersal, instead relying on use of nearby habitat. Reoccupation of inactive territories was the most common mechanism of new group formation in one population (Doerr et al. 1989), but territories that had been inactive for two years were rarely recolonized. Dispersing birds may therefore not find and recolonize isolated sites as readily as sites closer to dispersal centers. Managed recruitment stands had a significantly higher isolation coefficient (II4000) than active clusters. If breeding pairs are translocated to these sites this may not be a problem, but reliance on natural dispersal for cluster formation and maintenance may not be successful when isolation coefficients are high.

Pasture and open water adjacent to a cluster negatively influenced its status. There were few cluster sites that had such apparently inimical neighboring land uses, but those that did were much more likely to be inactive than active. Thus, fragmentation of forest, and especially of forest ownership, can have this added negative impact on Red-cockaded Woodpecker status. In addition, the absence of a timber corridor from one cluster site to another was a negative factor on cluster status: active clusters were more likely to be connected to other clusters by corridors of

pine sawtimber and/or poletimber, even circuitous ones, than inactive sites were. Red-cockaded Woodpeckers have been observed using seed trees or shelterwood in cutover areas for cavity construction (Conner et al. 1991), so it is not unreasonable to assume that such trees can also provide dispersal corridors.

The Red-cockaded Woodpecker will only recover to sustainable population levels if suitable habitat is available, and the suitability will depend on spatial, as well as timber, characteristics. When selecting stands for remedial work, those with the greatest potential for becoming and remaining active clusters should be considered first. The selection process should include determination of isolation measures, neighboring land uses, and connectivity among cluster sites.

ACKNOWLEDGMENTS

I thank L. H. Bonner, K. D. Baker, D. C. Bieber, R. N. Conner, and D. C. Rudolph with the U.S. Forest Service for their help with this project. I also acknowledge the support of S. F. Atkinson of the University of North Texas. This research was made possible by a cost-share agreement with the U.S. Forest Service, Lufkin, Texas, and a Research Opportunities Program grant from the University of North Texas. Thanks also to D. A. Schaefer, D. C. Rudolph, R. G. Hooper, and R. N. Conner for their constructive criticism and helpful comments on earlier drafts of this manuscript.

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Wilson Bull., 107(4), 1995, pp. 615–628

ARE RED-TAILED HAWKS AND GREAT HORNED OWLS DIURNAL-NOCTURNAL DIETARY COUNTERPARTS?

Carl D. Marti[1] and Michael N. Kochert[2]

Abstract.—Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (*Bubo virginianus*) are common in North America where they occupy a wide range of habitats, often sympatrically. The two species are similar in size and have been portrayed as ecological counterparts, eating the same prey by day and night. We tested the trophic similarity of the two species by comparing published dietary data from across the United States. Both species ate primarily mammals and birds, and mean proportions of those two prey types did not differ significantly between diets of the two raptors. Red-tailed Hawks ate significantly more reptiles, and Great Horned Owls significantly more invertebrates. Dietary diversity was not significantly different at the level of prey taxonomic class, and diet overlap between the two species averaged 91%. At the prey species level, dietary overlap averaged only 50%, and at that level Red-tailed Hawk dietary diversity was significantly greater than that of Great Horned Owls. Mean prey mass of Red-tailed Hawks was significantly greater than that of Great Horned Owls. Populations of the two species in the western United States differed trophically more than did eastern populations. We conclude that, although the two species are generalist predators, they take largely different prey species in the same localities resulting in distinctive trophic characteristics. *Received 19 December 1994, accepted 15 May 1995.*

Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (*Bubo virginianus*) have been portrayed as ecological counterparts that take the same kinds of prey by day and night (Bent 1938, Craighead and Craighead 1956, Austing 1964, Austing and Holt 1966, Springer and Kirkley 1978). Both are widespread, common raptors in North America (Johnsgard 1988, 1990), and both occupy a wide range of habitats, often sympatrically. They are similar in size (Red-tailed Hawk mean mass = 1126 g; Great Horned Owl mean mass = 1354 g; Dunning 1984), and both are considered to have generalized diets, i.e., they do not specialize on specific prey types (Errington et al. 1940, Steenhof and Kochert 1985).

Coexisting species segregate their feeding niches primarily by differences along three dimensions: the habitat used for foraging, the kind of food eaten, and the time of day that foraging occurs (Cody 1968, Schoener 1974, Jaksić 1988). Schoener (1974) considered time of activity to be the least influential of these niche dimensions, and Jaksić (1982) concluded that time of activity was not adequate to separate niches of hawks and owls. However, judging from the similarity in body size and habitat

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usage between Red-tailed Hawks and Great Horned Owls (Hagar 1957, McInvaille and Keith 1974, Houston 1975, Petersen 1979, Minor et al. 1993), time of foraging activity seems likely to be the most important factor differentiating the niches of the two.

Our objective was to determine if trophic characteristics of the two species support the contention that they are dietary counterparts. We tested whether time of activity produced substantial differences in trophic characteristics between the two raptors.

METHODS

We searched the literature for dietary data with the requirement that the geographic area and date of data collection potentially enabled both species to exploit the same prey resources. Additionally, we required that each sample contained at least 100 prey items, and had vertebrate prey identified to genus or species, and most invertebrate prey to order. For geographic analyses, we considered samples from New York, New Jersey, Connecticut, Ohio, Wisconsin, and Michigan as representing eastern populations, and samples from Wyoming, Utah, Idaho, Montana, Washington, and California as representing western populations. We calculated the following trophic estimators from the selected data sets: (1) Food-niche breadth (FNB) as estimated by Levins' (1968) modification of Simpson's index (FNB $= 1/\Sigma p_i^2$, where p_i = the frequency of each prey type in a diet) was calculated at both coarse and fine resolution. The coarse level (FNB_{cl}), where prey categories were taxonomic classes, provided an indication of the versatility of the predator, i.e., larger values at this level indicate that the predator is capable of detecting, capturing, and handling diverse kinds of prey (Greene and Jaksić 1983). The fine resolution (FNB_{sp}), where prey categories were species or genera for vertebrate prey and order for invertebrate prey, provided greater discrimination between the two raptors' diets. (2) Geometric mean prey mass (GMPM; Sokal and Rohlf 1981, p. 42) was estimated using prey weights in Steenhof (1983).

Overlap between diets of the two raptors was assessed by Pianka's index (1973): $O = \Sigma p_i \Sigma q_i / (p_i^2 \Sigma q_i^2)^{1/2}$, where p_i = the frequency of a prey type in one of the raptor's diet and q_i = the frequency of the same prey type in the other raptor's diet. Overlap was also calculated at coarse and fine resolutions using the same criteria as for FNB. Paired *t*-tests were used to compare means of trophic estimators.

RESULTS

The thirteen data sets meeting our selection criteria (Appendix 1) revealed that both Red-tailed Hawks and Great Horned Owls fed largely on vertebrates in five taxonomic classes, but they also consumed small numbers of arthropods. Mammals were numerically dominant in all of the Great Horned Owl diets, and in all but one Red-tailed Hawk diet (Fig. 1; Orians and Kuhlman 1956). Avian prey was second in numeric importance overall for both species (Fig. 1), but was exceeded by reptiles in four studies on the Red-tailed Hawk (Fitch et al. 1946, Knight and Erickson 1976, Fitzner et al. 1981, Marti et al. 1993b), and by arthropods in three studies on the Great Horned Owl (Fig. 1; Fitch 1947, Smith and

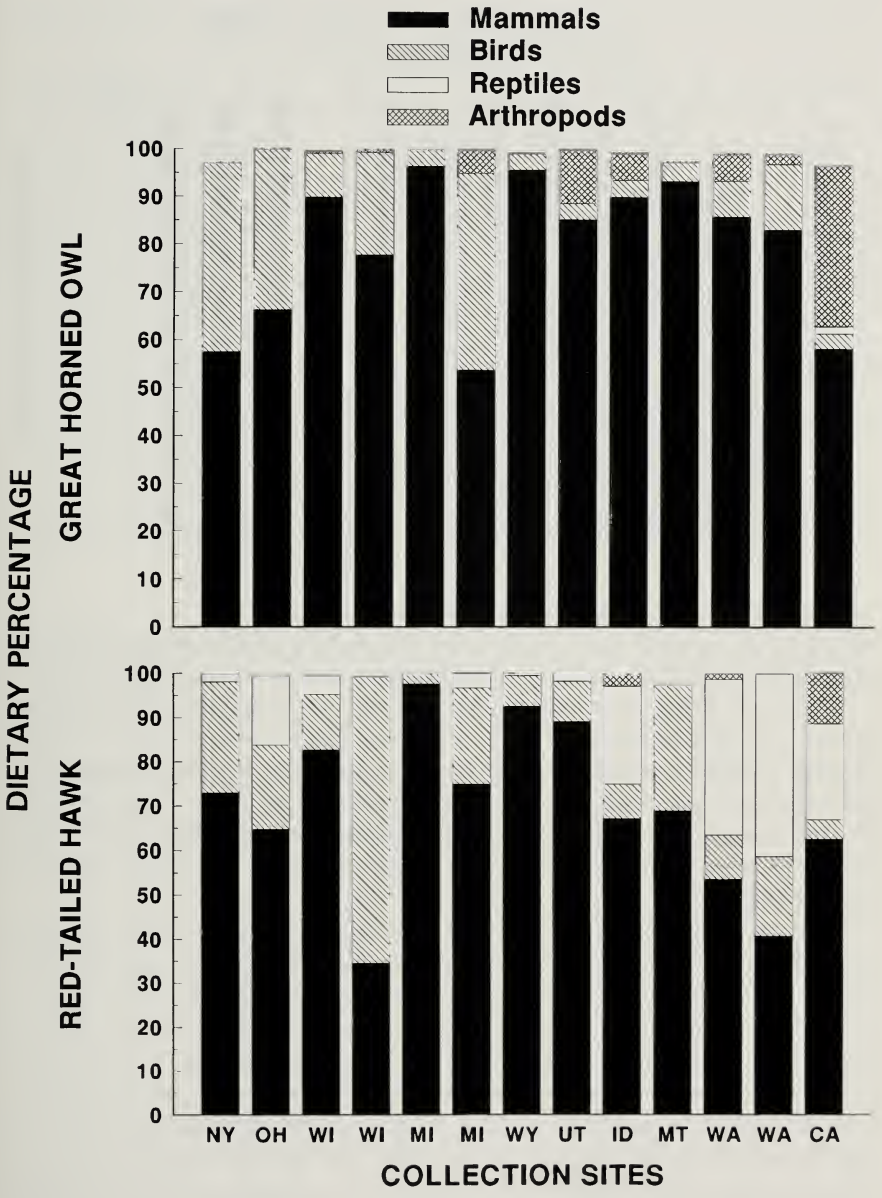

FIG. 1. Proportions by number of major prey types in diets of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

TABLE 1

SUMMARY AND COMPARISON OF TROPHIC CHARACTERISTICS OF GREAT HORNED OWLS AND RED-TAILED HAWKS (CALCULATED FROM DATA SOURCES IN APPENDIX I)

Trophic characteristic	Great Horned Owl		Red-tailed Hawk			
	Mean	SD	Mean	SD	t^a	*P*
Food-niche breadth (class)	1.51	0.42	1.78	0.49	1.81	0.10
Food-niche breadth (species)	5.44	3.28	6.66	4.58	2.36	0.04
Geometric mean prey mass, g	76.0	64.7	175.0	137.4	3.00	0.01
% mammals in diet	79.5	15.3	69.4	18.9	1.73	0.11
% birds in diet	14.2	14.2	17.7	16.3	0.77	0.46
% reptiles in diet	0.4	0.8	11.4	14.5	2.80	0.02
% amphibians in diet	0.1	0.4	0.2	0.3	0.25	0.81
% fishes in diet	0.5	1.0	0.2	0.5	1.43	0.18
% arthropods in diet	5.0	9.3	1.2	3.2	2.15	0.05
Mean overlap in prey class (SD)	0.91 (0.1)					
Mean overlap in prey species (SD)	0.50 (0.3)					

[a] Paired *t*-tests, N = 13.

Murphy 1973, Marti et al. 1993b). Although both raptors occasionally ate amphibians and fish, neither was important in their diets (Table 1).

The heavy reliance on mammalian prey by both raptors resulted in high dietary overlap between them at the prey class level (Fig. 2). Dietary overlap at the prey species level was considerably lower indicating that the two often ate different mammal species at the same localities (Fig. 2). The most common prey for Red-tailed Hawks typically was a diurnal mammal while for Great Horned Owls it was a nocturnal mammal (Table 2).

FNB_{cl} was also quite similar between the two species demonstrating that they have corresponding capabilities in detecting and capturing prey at the broad category of taxonomic class (Fig. 3). Mean differences between FNB_{cl} in paired samples of Red-tailed Hawks and Great Horned Owls were not significant (Table 1). FNB_{cl} of the Red-tailed Hawk was larger than the Great Horned Owl FNB_{cl} in eight of the paired samples, but the converse was true in five. FNB_{sp} of the Red-tailed Hawk was significantly greater than that of the Great Horned Owl (Table 2). Ten of the 13 paired FNB_{sp} values were higher for the hawk (Fig. 4), showing that it usually preyed upon a greater diversity of prey species than did the owl. Red-tailed Hawks took larger prey on average in 11 of the 13 paired samples (Fig. 5), and the GMPM of the Red-tailed Hawk overall was significantly larger than that of the Great Horned Owl (Table 1).

In dietary samples from eastern populations, none of the trophic char-

FIG. 2. Overlap between diets of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

TABLE 2

MOST COMMON PREY FOR GREAT HORNED OWLS AND RED-TAILED HAWKS (CALCULATED FROM DATA SOURCES IN APPENDIX I)

Location[a]	Most common prey in diet	
	Great Horned Owl	Red-tailed Hawk
1	*Peromyscus*	*Tamias* and *Sciurus*
2	*Microtus*	*Tamias*
3	*Peromyscus*	*Spermophilus*
4	*Peromyscus*	*Phasianus*
5	*Peromyscus*	*Microtus*
6	*Microtus*	*Microtus*
7	*Microtus*	*Spermophilus*
8	*Lepus*	*Lepus*
9	*Microtus*	*Spermophilus*
10	*Peromyscus*	*Spermophilus*
11	*Perognathus*	*Spermophilus*
12	*Microtus*	*Coluber*
13	*Neotoma*	*Spermophilus*

[a] See Appendix I for geographic location and source of data.

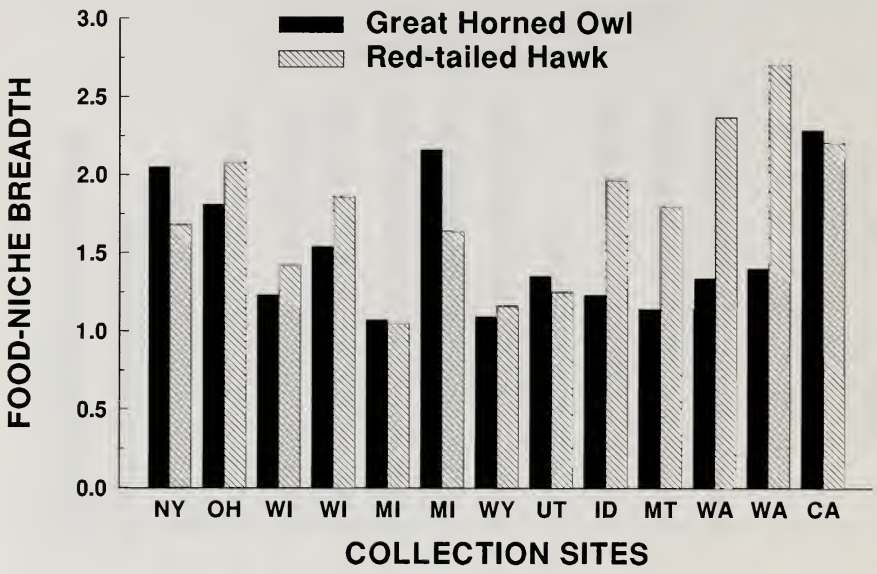

FIG. 3. Dietary diversity at the coarse level of prey discrimination (FNB_{cl}) in diets of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

acteristics we measured was significantly different between the two species (Table 3). In the West, though, five of the seven trophic characteristics did differ significantly. GMPM diverged most with Red-tailed Hawks taking significantly larger prey. Dietary overlap at the prey species level also was much less in the West indicating a stronger divergence in the kinds of prey eaten (Table 3). Despite the geographic variation in interspecific differences between Red-tailed Hawks and Great Horned Owls, intraspecific trophic characteristics were not significantly different, east versus west, except for birds in diets of Great Horned Owls (Table 4).

DISCUSSION

Red-tailed Hawks and Great Horned Owls appear to use similar habitats, although we do not know of any studies that simultaneously examined microhabitat use by the two species. Numerous investigators found them breeding in the same habitat (e.g., Hagar 1957, McInvaille and Keith 1974, Houston 1975, Petersen 1979, Minor et al. 1993). Nests of the two species averaged only 51 m apart where nest sites were limited and clumped (Houston 1975), but even in more homogeneous habitats the two often nested within 200–300 m of each other (Hagar 1957, McInvaille and Keith 1974, Minor et al. 1993). Great Horned Owls commonly use

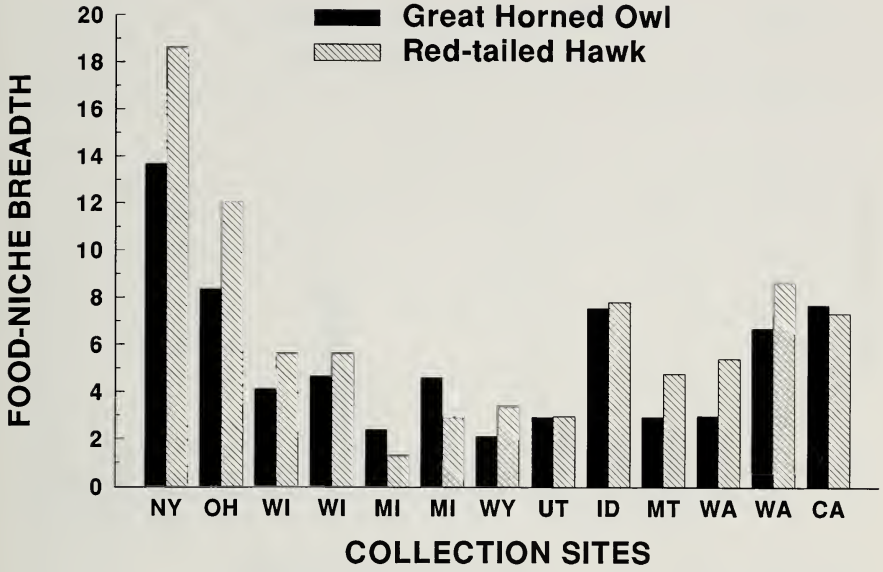

FIG. 4. Dietary diversity at the fine level of prey discrimination (FNB_{sp}) in diets of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

nests constructed by Red-tailed Hawks (Orians and Kuhlman 1956, Hagar 1957, Houston 1975, Petersen 1979, Minor et al. 1993).

Both of these raptors are dietary generalists and highly opportunistic predators capable of taking the same prey over a large range in size and type. They have the potential to have high overlap in diet, and on a continent-wide basis we found that diets of co-occurring populations did overlap extensively at the coarse level of prey discrimination (taxonomic class of prey). At the fine level (prey species), however, their diets on average overlapped only 50%—a large niche separation. Both species have been reported to feed on carrion (Sooter 1942, Stalmaster 1980, Preston and Beane 1993). How this behavior might affect the trophic parameters we measured cannot be evaluated because the data on it are limited and mostly anecdotal.

Trophic differences between the two species were much more pronounced in the West than in the East. A previous broad-scale analysis of the trophic structure of raptor assemblages (Marti et al. 1993a) concluded that, on a regional basis, both the Red-tailed Hawk and Great Horned Owl consumed far more species of prey and had broader food-niche breadths in the western United States than in the central or eastern U.S. That same pattern held for entire assemblages of many raptor species

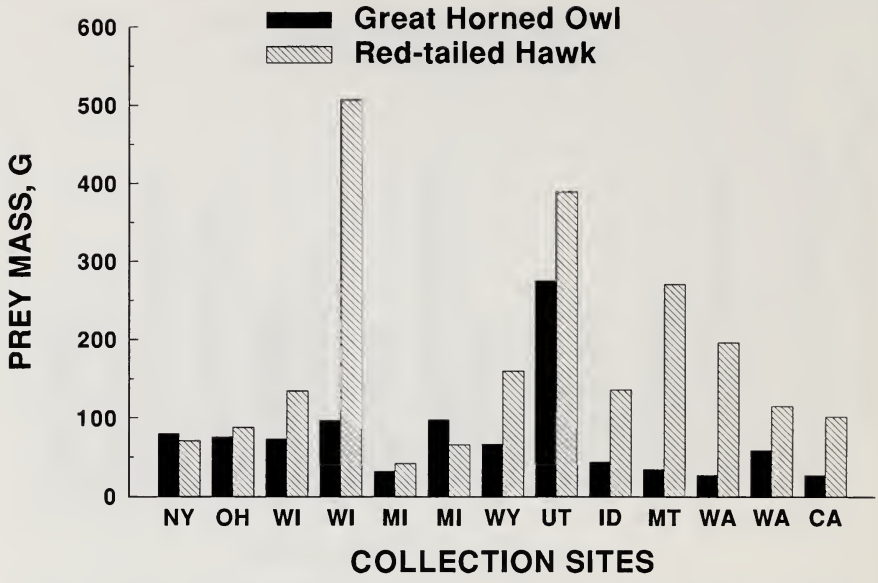

FIG. 5. Geometric mean prey mass of Great Horned Owls and Red-tailed Hawks. Collection sites are arranged from east to west and correspond to the order of data sets in Appendix I.

(Marti et al. 1993a). The species density of both birds and mammals increases from east to west in North America (Cook 1969, Pagel et al. 1991), and, at least for mammals, the size of geographic ranges decreases toward the West. These patterns could help explain why raptor food-niche breadths calculated for large regions should be broader in the West than in the East. Our present much finer scale analysis found that food-niche breadth was narrower for both Red-tailed Hawks and Great Horned Owls in the West compared to the East. A possible explanation is that greater diversity of available prey in the West may permit local populations of these two raptors to increase their diet segregation in that region.

Jaksić (1982) believed that time of activity, in general, did not result in diet differences sufficient to separate the niches of hawks and owls. Carothers and Jaksić (1984) proposed that interference competition rather than exploitation competition was the force causing the diel difference in activity between hawks and owls. Time of activity, however, does seem to be the niche dimension that causes the greatest divergence in diets of Red-tailed Hawks and Great Horned Owls. Our findings show that diets of the two species at the same locality are similar to each other in most trophic characteristics, but that these two raptors concentrate their pre-

TABLE 3

TROPHIC CHARACTERISTICS OF GREAT HORNED OWLS (GHO) VERSUS RED-TAILED HAWKS (RTH) IN EASTERN AND WESTERN POPULATIONS (CALCULATED FROM DATA SOURCES IN APPENDIX I)

Trophic characteristic	Eastern U.S.		Western U.S.	
	GHO	RTH	GHO	RTH
Food-niche breadth (class)				
Mean (SD)	1.64 (0.44)	1.62 (0.36)	1.41 (0.41)	1.92 (0.57)
Paired-*t* (*P*)[a]	0.15 (0.89)		2.44 (0.05)	
Food-niche breadth (species)				
Mean (*P*)	6.30 (4.10)	7.70 (6.49)	4.70 (2.48)	5.77 (2.22)
Paired-*t* (*P*)	1.32 (0.24)		2.44 (0.05)	
Geometric mean prey mass, g				
Mean (*P*)	75.2 (23.8)	151.1 (177.0)	76.1 (88.9)	195.4 (102.9)
Paired-*t* (*P*)	1.10 (0.32)		5.03 (0.002)	
% mammals in diet				
Mean (SD)	73.6 (17.3)	71.2 (21.4)	84.6 (12.4)	67.8 (18.4)
Paired-*t* (*P*)	0.25 (0.81)		2.39 (0.05)	
% birds in diet				
Mean (SD)	24.3 (15.5)	24.2 (21.4)	5.6 (3.9)	12.1 (8.4)
Paired-*t* (*P*)	0.01 (0.99)		2.16 (0.07)	
% reptiles in diet				
Mean (SD)	0.1 (0.2)	4.2 (5.8)	0.7 (1.0)	17.6 (17.1)
Paired-*t* (*P*)	1.71 (0.15)		2.66 (0.04)	
% arthropods in diet				
Mean (*P*)	1.0 (2.0)	0 (0)	8.5 (11.9)	2.2 (4.2)
Paired-*t* (*P*)	— (—)		2.05 (0.09)	
Mean overlap in prey class (SD)	0.92 (0.1)		0.90 (0.1)	
Mean overlap in prey species (SD)	0.58 (0.2)		0.42 (0.3)	

[a] N = 13.

dation on a different array of species by being active at different times of the day.

Other sympatric predators (raptors, mammals, and snakes) that eat the same species taken by Red-tailed Hawks and Great Horned Owls must also be considered when attempting to understand and compare the niches of Red-tailed Hawks and Great Horned Owls. Only four predator assemblages in North America containing both Red-tailed Hawks and Great Horned Owls have been analyzed for such effects (Jaksić 1988, Marti et

TABLE 4

TROPHIC CHARACTERISTICS OF EASTERN VERSUS WESTERN POPULATIONS OF GREAT HORNED OWLS AND RED-TAILED HAWKS[a]

Trophic characteristic	Great Horned Owl						Red-tailed Hawk					
	Eastern		Western				Eastern		Western			
	$\bar{x}$	(SD)	$\bar{x}$	(SD)	t	P	$\bar{x}$	(SD)	$\bar{x}$	(SD)	t	P
Food-niche breadth (class)	1.64	(0.44)	1.41	(0.41)	0.86	0.41	1.62	(0.36)	1.92	(0.57)	0.74	0.47
Food-niche breadth (species)	6.30	(4.10)	4.70	(2.48)	1.01	0.33	7.70	(6.49)	5.77	(2.22)	1.12	0.29
Geometric mean prey mass	75.2	(23.8)	76.1	(88.9)	0.01	0.99	151.1	(177.0)	195.4	(102.9)	0.56	0.58
% mammals in diet	73.6	(17.3)	84.6	(12.4)	1.33	0.21	71.2	(21.4)	67.8	(18.4)	0.31	0.76
% birds in diet	24.3	(15.5)	5.6	(3.9)	3.10	0.01	24.2	(21.4)	12.1	(8.4)	1.39	0.19
% reptiles in diet	0.1	(0.2)	0.7	(1.0)	1.33	0.21	4.2	(5.8)	17.6	(17.1)	1.81	0.10
% arthropods in diet	1.0	(2.0)	8.5	(11.9)	1.50	0.16	0	—	2.2	(4.2)	—	—

[a] Calculated from data sources in Appendix I.

al. 1993b). In two assemblages (Idaho and Wisconsin) the two species were in different feeding guilds, but in the other two (Michigan and California) they were in the same guild (in California they were in different subgroups within one guild). The small number of such studies does not provide much insight into what trophic patterns might arise out of interactions among a wider range of predators. But, those analyses may indicate that trophic relationships between Red-tailed Hawks and Great Horned Owls are also affected by the presence of other predators.

The high overlap in habitat use and prey between Red-tailed Hawks and Great Horned Owls could certainly lead to exploitation competition. Competition and its effects, however, have been notoriously hard to quantify in most bird populations (Wiens 1989). We know of only two studies on competition in raptors that have detected reduced reproductive success in the presence of a potentially competing species (Nilsson 1984, Korpimäki 1987). Interference competition between Red-tailed Hawks and Great Horned Owls may be largely avoided by differences in time of activity. However, Great Horned Owls begin nesting about one month earlier than co-existing Red-tailed Hawks (Orians and Kuhlman 1956, Seidensticker and Reynolds 1971, McInvaille and Keith 1974, Minor et al. 1993) and may thus interfere with the hawks' access to breeding areas by appropriating nests. The ultimate form of interference competition—one species killing the other—has been reported between these two species, mostly based on circumstantial evidence. The majority of instances were Great Horned Owls preying on nestling Red-tailed Hawks (Hamerstrom and Hamerstrom 1951, Craighead and Craighead 1956, Luttich et al. 1971, Petersen 1979), but one adult Red-tailed Hawk may have been killed by a Great Horned Owl (Houston 1975). Red-tailed Hawk predation on nestling Great Horned Owls was suspected by Fitch (1940) and Orians and Kuhlman (1956).

Our analysis suggests that time of activity may be the most important factor that prevents or reduces the degree of competition between these two species by permiting sympatric populations to prey upon somewhat different prey arrays. Our results further support the contention that many raptors are very versatile in diet, and that diets in local areas are, to a large extent, the result of opportunism.

The answer to the question—are these two species diurnal-nocturnal dietary counterparts—is strongly affected by the scale used to compare them. At a coarse level, the two are much alike in habitat use and predatory capability, and could be considered to be day-night equivalents. At a fine level, dietary differences are much more pronounced. Thus, Red-tailed Hawks and Great Horned Owls, by being active at different times,

interact with different arrays of prey species, and are not day-night feeding equivalents.

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APPENDIX I

SOURCES AND CHARACTERISTICS OF DATA SETS USED FOR ANALYSES

	Location	Habitat type	Length of study (years)	Season of data collection	Source
1	New York, New Jersey, Connecticut	Deciduous forest	12	Breeding	Bosakowski and Smith (1992)
2	Ohio	Farmland	3	Breeding	Springer and Kirkley (1978)
3	Wisconsin	Farmland	3	All year	Errington (1932, 1933)
4	Wisconsin	Farmland	3	Breeding	Orians and Kuhlman (1956)
5	Michigan	Farmland	2	Winter	Craighead and Craighead (1956)
6	Michigan	Farmland	2	Breeding	Craighead and Craighead (1956)
7	Wyoming	Mountain valley[a]	1	Breeding	Craighead and Craighead (1956)
8	Utah	Shrub-steppe	4	Breeding	Smith and Murphy (1973)
9	Idaho	Shrub-steppe	17	Breeding	Marti et al. (1993b)
10	Montana	Mountain valley[a]	3	Breeding	Seidensticker (1968, 1970)
11	Washington	Shrub-steppe	6	Breeding	Fitzner et al. (1981)
12	Washington	Shrub-steppe	2	Breeding	Knight and Erickson (1976, 1977)
13	California	Grassland/chaparral	3	All year	Fitch et al. (1946), Fitch (1947)

[a] Mostly riparian and shrub-steppe with some upland forest and pasture.

Wilson Bull., 107(4), 1995, pp. 629–640

FEEDING BEHAVIOR, PREY SELECTION, AND BILL SIZE OF PIED AND SOOTY OYSTERCATCHERS IN AUSTRALIA

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Abstract.—We studied the relationships between feeding behavior, prey selection and bill size for sympatric Pied (*Haematopus longirostris*) and Sooty (*H. fuliginosus*) Oystercatchers feeding at Australian intertidal mudflats. Foraging Sooty Oystercatchers used a rapid pecking behavior for a greater proportion of time and used a slow pecking behavior for a lesser proportion of time as compared to Pied Oystercatchers. Within each species males used a rapid pecking behavior for more time and used a slow pecking behavior for less time than females. As rapid pecking was used mainly for the capture of crabs, snails and bivalves while slow pecking was used mainly for the capture of polychaete worms, the diet of Sooty Oystercatchers contained significantly more hard-shelled prey and less soft-bodied prey than Pied Oystercatchers. For each species, males took more hard-shelled prey and fewer worms than females. Thus, species and sexual differences in foraging behavior and prey selection segregated the foraging roles of Pied and Sooty Oystercatchers, potentially reducing competition, facilitating their coexistence. A general pattern for oystercatchers is that longer bill length is associated with higher percentages of soft-prey in the diet for different species, and for sexes within species. A comparison of bill lengths indicated that in Tasmania Sooty Oystercatchers had longer bills than Pied Oystercatchers and within each species, females had longer bills than males. Thus, our results for species are counter to general expectations while results for sexes are consistent with general patterns. *Received 28 July 1994, accepted 20 May 1995.*

The Oystercatchers are a cosmopolitan family of shorebird (Charadriiformes: Haematopodidae) whose species exhibit a general pattern with regard to foraging habitat, prey selection and bill size. Uniformly black species forage more commonly on hard substrates at rocky coastal habitat and have higher percentages of hard-shelled prey than soft-bodied prey in their diet (Bent 1929, Baker 1974, Hartwick 1974, Considine 1979, Hockey and Underhill 1984, Lane 1987, Lauro 1994) compared to pied species (dark upper torso with a white belly) who forage primarily on soft substrates at estuaries (Bent 1929; Heppleston 1972; Baker 1974; Goss-Custard and Durell 1983, 1987; Nol 1984; 1985; Lane 1987; Lauro 1994). Black species generally have shorter bills and larger bodies when compared to pied species (Baker 1974, 1975; Nol 1984).

Within all species of oystercatchers, females on average have longer bills than males (Heppleston 1970; Baker 1974, 1975; Hockey 1981;

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Swennen et al. 1983; Hulscher 1985; Jehl and Murray 1986; Hulscher and Ens 1992; Durell et al. 1993; Marchant and Higgins 1993; Lauro 1994). This sexual dimorphism has been correlated with differences in foraging ecology with females capturing higher percentages of soft-bodied than hard-bodied prey as compared to males (Heppleston 1970, Dare 1977, Swennen et al. 1983, Hockey and Underhill 1984, Hulscher 1985, Hulscher and Ens 1992, Durell et al. 1993, Lauro 1994).

Thus, for oystercatchers it may be the case that shorter bill length is better adapted for capturing hard prey, especially off rock, while longer bill length may be better adapted to capturing soft-bodied prey submerged in mud, especially soft-bodied prey (Baker 1974, Nol 1984, Lauro 1994). In addition, species and sexual differences in the foraging ecology, correlated with bill length, may act to ecologically segregate Black and Pied oystercatchers where they occur in sympatry.

This study compares the foraging behavior and prey selection of Pied (*H. longirostris*) and Sooty (*H. fuliginosus*) Oystercatchers in Tasmania, Australia. At the Furneaux Islands, where this study takes place, Pied Oystercatchers fed only on intertidal mudflat while Sooty Oystercatchers fed at rocky shores as well as intertidal mudflats (Lauro 1994). We compare foraging ecology for the two species at overlapping feeding territories on intertidal mudflat adjacent to nesting areas. In addition, we compare bill sizes for species and for sexes within species using museum specimens and information presented in Marchant and Higgins (1993). Our objective is to determine what mechanisms, if any, existed to subdivide the foraging roles of the two sympatric species during the breeding season. We discuss the extent to which bill length and species specific behavior predict foraging behavior and prey selection.

STUDY AREA AND METHODS

We conducted field studies in the austral spring and summer of 1989/1990 on Big Green Island (40°11′S, 147°59′E) at the Furneaux Islands, Tasmania, Australia. Big Green Island is 3 km west of the village of Whitemark on Flinders Island (the main island of the Furneaux Group) and is 122 ha in area. Pied and Sooty Oystercatchers were territorial and excluded conspecifics from nesting areas along the beach and at feeding sites adjacent to nesting locations. Therefore, it was possible to identify pairs by breeding location. The identity of feeding individuals was confirmed by watching birds return to nest sites, change positions with incubating mates or by association with chicks. In addition, the feeding territories for the two species were overlapping, and although interspecific competition was observed, one species did not exclude the other (Lauro, pers. obs.).

Oystercatchers can be sexed based on bill and body size (Considine 1979, Hockey 1981, Hayman et al. 1986). For this study individuals of breeding pairs were sexed by comparing them together during observations and by position during copulation. Female oystercatchers of both species were larger, had browner backs, and longer bills than males (Considine 1979).

Ten-minute observations of feeding individuals in nesting pairs were made over the breeding season from observation blinds, using a 10 × 20 telescope. No distinction was made for the stage of the breeding season. Observations were recorded on a laptop computer using a BASIC program that chronologically recorded all feeding behaviors and prey captured. From these data calculations were made for the proportion of times using different feeding behaviors, pecks per minute, and handling times for different prey types. In addition, we tallied the number of different prey groups captured during the 10-min observation periods.

Prey captured by oystercatchers was identified by observation in the field and classified into the following groups (since it was not always possible to identify to species): snails, mussels, other bivalves, polychaete worms, crabs, and surface items. Surface items were prey that were picked off the surface and could not be identified because they were too small to see.

The range of 10-min observation periods was 1–5 and we used weighted means for each individual for the analysis of proportion data. The distributions of the proportion data were not normal and contained many zeros. In this situation no statistical test is exact (Sokal and Rohlf 1995). The data were analyzed using two different methods: (1) non-parametric tests, and (2) analysis of variance (ANOVA). The results from the two methods were similar. We use ANOVA's for statistical tests because they are robust when assumptions of normality are not met (Sokal and Rohlf 1995) and because, in some cases, of the value of interpreting the interaction term between species and sex. Distribution of the data for bill dimensions was normal or near normal justifying ANOVA, and transformation of data (e.g., log-transformation) did not change the significance levels of ANOVA's. Analyses reported hence are for untransformed data.

Intertidal mudflats were sampled to compare relative proportions of prey groups available to the proportion of prey groups captured by oystercatchers. Every 20 m along the 1.7 km stretch of beach where birds nested, a 0.25 m × 0.25 m quadrat was randomly placed on a transect from the high to low tide line. Data collected for rocky sections of the beach were not included in the analysis since birds rarely used these habitats for feeding. The distance at which the quadrat was placed along the transect was determined using a random numbers table. Quadrats were selectively sampled for known prey of oystercatchers. This included invertebrates recorded as prey (turbellarians, amphipods and isopods) from another study of the foraging ecology of Sooty Oystercatcher (Considine 1979), since these would be likely prey of Sooty Oystercatchers at the Furneaux Islands. Prey were identified using guides to Australian coastal invertebretates (MacPherson and Gabriel 1962, Phillips et al. 1984).

Within each quadrat potential prey items were recorded to a depth of 90 mm (estimated maximum depth that an oystercatcher bill can reach). For each quadrat a summation was made for prey located at the surface and for prey located below the surface. The total number of different prey items below the surface was estimated based on the number of different species found in a mud sample core and the volume of an entire quadrat. The size of the cylindrical core was 120 mm in diameter and 90 mm deep. For each quadrat, invertebrates were categorized into the same prey groups used by oystercatchers.

Manly's alpha indices (Manly 1974) for preference were used to compare the relative proportion of prey in the diet of the species and sexes to that which was available on intertidal mudflats.

We measured bills of museum specimens from the Royal Ontario Museum (ROM) and the American Museum of Natural History (AMNH). Our measurements included: (1) length from the bill tip to the base of the head on the dorsal side where feathers start to grow (i.e., exposed culmen), and (2) width and depth measured at the center of nasal opening at the base of the bill. The distribution of data for bill characters was normal or near normal justifying the use of analysis of variance (ANOVA) for data interpretation. In addition, we

evaluate data presented in Marchant and Higgins (1993) for bill dimensions for Pied and Sooty Oystercatchers. Since we did not have the raw data for information presented in Marchant and Higgins (1993) we do one-way ANOVA's for unplanned comparisons and Tukey Kramer multiple comparison tests (Sokal and Rohlf 1995).

RESULTS

Two distinct behaviors were used by both species while feeding on the intertidal mudflat: slow pecking and rapid pecking. Slow-pecking birds moved with a regular pace over the mudflat when feeding while rapid-pecking birds would concentrate their efforts in a small area and then move to a new spot. A slow-pecking bird would move across the mudflat apparently searching visually for sites to test for the presence of worms. Birds would appear to see a likely spot, touch their bill to the surface (a peck) and, on detection, probe into the mud for capture. The probing action for worms was often very quick and birds did not always place their bills deep into the mud. Therefore, it was difficult to differentiate a peck from a probe so we recorded only pecks and not the final probe that resulted in prey capture.

Birds that used the rapid pecking behavior appeared to depend less on visual cues and more on tactile cues. Remaining fairly stationary birds moved their bills up and down on the surface to cover as much area as possible to detect prey covered by weed or a film of mud. The rapid pecking behavior was generally associated with the capture of hard-shelled prey such as crabs and snails (that were hammered open) and with the capture of small, usually unidentifiable surface items.

Sooty Oystercatchers used the rapid pecking behavior for a significantly greater proportion of time and used the slow pecking behavior for a significantly lesser proportion of time than did Pied Oystercatchers (Table 1). When slow pecking, Sooty Oystercatchers had a lower peck rate than Pied Oystercatchers, probably because they spent more time walking in search of sites to use the rapid pecking behavior and less time actually foraging (Table 1). Peck rates were not compared during the rapid pecking behavior because the pecks occurred too quickly to record accurately. No differences in prey handling times occurred between species (Table 1).

The diet of Sooty Oystercatchers was broader than that of Pied Oystercatchers and included all prey groups (Table 2; Fig. 1). Sooty Oystercatchers had a higher percentage of hard-shelled prey in their diet than Pied Oystercatchers (Table 2; Fig 1) because they commonly fed on crabs and snails. Pied Oystercatchers were never observed to eat these prey and fed mainly on worms (Table 2; Fig 1). Consequently, Sooty Oystercatchers had significantly fewer worms in their diet as compared to Pied Oystercatchers (Table 2; Fig. 1).

TABLE 1

A COMPARISON OF FEEDING BEHAVIOR BETWEEN SPECIES AND SEXES[a]

Behavior	Sooty Oystercatchers		Pied Oystercatchers	
	Male $\bar{x} \pm$ SE	Female $\bar{x} \pm$ SE	Male $\bar{x} \pm$ SE	Female $\bar{x} \pm$ SE
Slow peck time[a] (% of total)	0.47 ± 0.098	0.60 ± 0.109	0.71 ± 0.125	0.93 ± 0.044
Rapid peck[a] (% of total)	0.53 ± 0.098	0.40 ± 0.109	0.29 ± 0.125	0.07 ± 0.044
Pecks/min. in slow-peck[b]	6.52 ± 1.938	10.47 ± 2.170	10.83 ± 2.353	19.15 ± 4.943
Handling time—worms (sec)	1.6 ± 0.18	1.9 ± 0.40	1.9 ± 0.30	2.6 ± 0.74
Handling time—crabs (sec)	11.4 ± 3.15	6.8 ± 2.87	—	—
N	12	12	10	11

[a] Species, $F_{1,41} = 8.83$, $P < 0.01$; sex, $F_{1,41} = 3.42$, $P < 0.05$; species × sex $F_{1,41} = 0.23$, $P > 0.05$ (NS).
[b] Species, $F_{1,41} = 10.31$, $P < 0.001$; sex, $F_{1,41} = 5.78$, $P < 0.02$; species × sex $F_{1,41} = 0.23$, $P > 0.05$ (NS).

Within each species males used the rapid pecking behavior more often and the slow pecking behavior less often than females (Table 1). Males of both species had a lower peck rate when using the slow peck behavior (Table 1) and captured significantly fewer worms compared to females (Table 2). Sooty Oystercatcher males had a greater proportion of crabs in their diet than females (Table 2, Fig. 1). Neither species showed a difference in prey handling times between sexes (Table 1).

When the proportion of prey captured was compared to the proportion

TABLE 2

PROPORTION OF DIFFERENT PREY TYPES CAPTURED FOR EACH SPECIES AND SEX

Food item	Sooty Oystercatcher		Pied Oystercatcher	
	Male $\bar{x} \pm$ SE	Female $\bar{x} \pm$ SE	Male $\bar{x} \pm$ SE	Female $\bar{x} \pm$ SE
Snails	0.08 ± 0.052	0.01 ± 0.003	—	—
Mussels	0.03 ± 0.028	0.01 ± 0.005	—	0.01 ± 0.001
Other bivalves	0.01 ± 0.005	0.00 ± 0.003	0.09 ± 0.093	—
Worms[a]	0.32 ± 0.084	0.76 ± 0.074	0.69 ± 0.155	0.93 ± 0.027
Crabs[b]	0.29 ± 0.074	0.07 ± 0.036	—	—
Surface items[c]	0.26 ± 0.071	0.15 ± 0.059	0.22 ± 0.142	0.06 ± 0.027
N	12	11	9	11

[a] Species, $F_{1,41} = 14.4$, $P < 0.0005$; sex, $F_{1,41} = 14.7$, $P < 0.0005$; species × sex, $F_{1,41} = 1.78$, $P > 0.05$ (NS).
[b] Sex, $t = 2.51$, $P = 0.02$.
[c] Species, $F_{1,41} = 5.39$, $P < 0.05$; sex, $F_{1,41} = 1.36$, $P > 0.05$ (NS); species × sex, $F_{1,41} = 0.62$, $P > 0.05$ (NS).

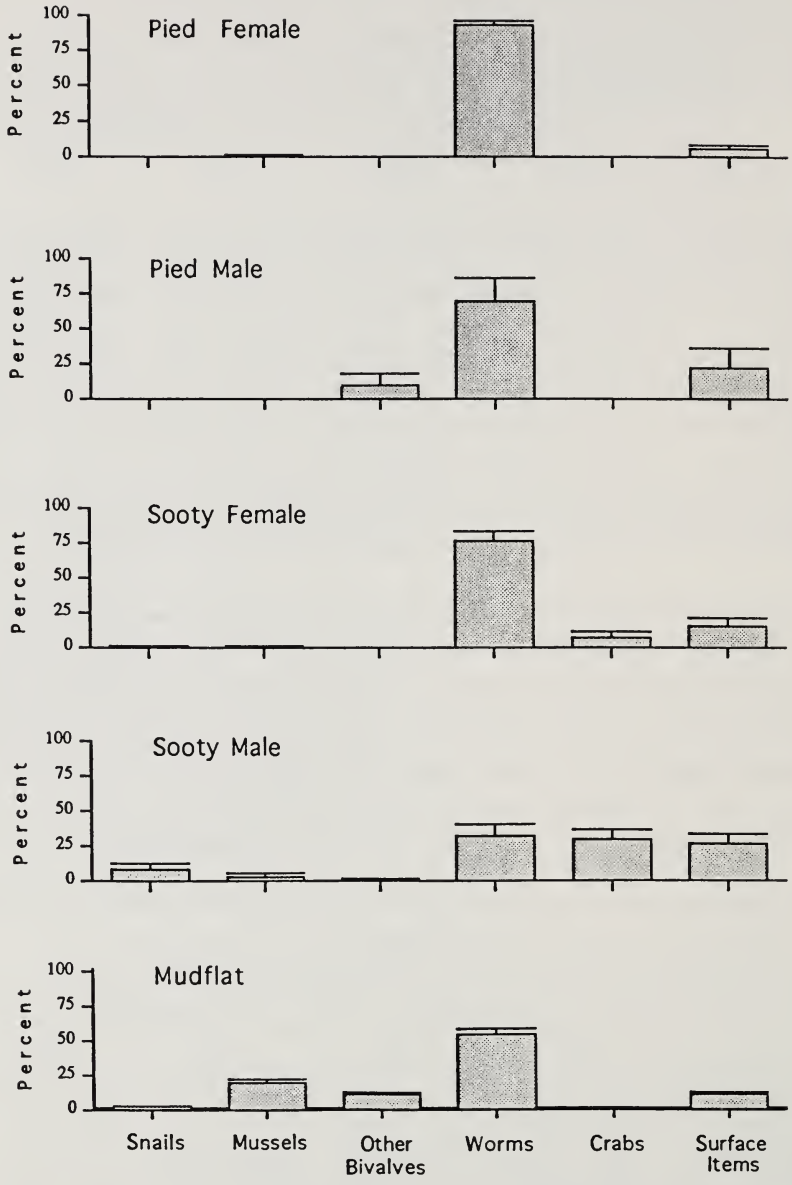

FIG. 1. A comparison of the percent of prey types taken by both sexes of Pied and Sooty Oystercatchers and of that recorded on the intertidal mudflat.

TABLE 3

PREFERENCES FOR PREY TYPES RELATIVE TO THAT AVAILABLE ON INTERTIDAL MUDFLAT USING MANLY'S ALPHA INDEX (MANLY 1974)[a]

	Sooty Oystercatcher		Pied Oystercatcher	
Prey type	Female	Male	Female	Male
Snails	0.03	0.08	0.00	0.00
Mussels	0.01	0.00	0.02	0.00
Other bivalves	0.00	0.07	0.00	0.20
Worms	0.15	0.02	0.73	0.31
Crabs	0.72	0.83	0.00	0.00
Surface items	0.09	0.00	0.24	0.49

[a] A preference for a prey type occurs when a value is above ⅙ or 0.17 (which equals 1/m where m is the number of prey groups). When a value of 0.17 occurs no preference is shown and values below 0.17 indicate the avoidance of a prey type.

of prey available on the intertidal mudflat, male and female Sooty Oystercatchers showed a preference for crabs (Table 3, Fig. 1). Pied Oystercatchers of both sexes were found to have a preference for worms and surface items but only Pied Oystercatcher males showed a preference for bivalves other than mussels (Table 3, Fig. 1).

Along the mainland coast, Pied Oystercatcher bill length appears to be longer than that of Sooty Oystercatchers (Table 4). However, data for museums specimens (ROM and AMNH) and information presented in Marchant and Higgins (1993) suggest that in Tasmania, Sooty Oystercatcher bill length is longer than Pied Oystercatcher bill length (Table 4). A one-way ANOVA for the four species/sex classes showed a significant difference for bill length ($F_{3,27} = 20.51$, $P < 0.0001$). If a Pied male is assigned a mean bill length of 1, then the relative mean bill lengths of Sooty male, Pied female, and Sooty female would be 1.09, 1.10 and 1.25 respectively. When a Tukey-Kramer multiple comparison test was conducted it was found that: bill length for Pied Oystercatcher males was significantly shorter than that for Sooty Oystercatcher males ($P < 0.05$); bill length for Sooty Oystercatcher males was not significantly different than that for Pied Oystercatcher females ($P > 0.05$); bill length for Pied Oystercatcher females was significantly shorter than that for Sooty Oystercatcher females ($P < 0.05$, Table 1).

For all data sets examined females within each species had longer bills than males (Table 4). No species or sexual differences were found for bill depth or width for data collected around the coastline (Table 4) or for the Tasmanian data (one-way ANOVA's, bill depth: $F_{3,27} = 1.37$, $P > 0.05$; bill width: $F_{3,27} = 0.01$ $P > 0.05$).

TABLE 4
A COMPARISON OF BILL DIMENSIONS (MM) BY SPECIES AND SEX

Variable	Sooty Oystercatcher		Pied Oystercatcher	
	Male $\bar{x} \pm$ SE	Female $\bar{x} \pm$ SE	Male $\bar{x} \pm$ SE	Female $\bar{x} \pm$ SE
Tasmania[a,b]				
Length	73.4 ± 1.16	83.6 ± 2.85	67.0 ± 3.83	73.9 ± 1.14
Depth	17.4 ± 0.48	17.6 ± 1.05	15.7 ± 0.78	16.1 ± 0.93
Width	15.6 ± 0.30	15.3 ± 0.53	—	—
N	7	8	8	8
All locations[c,d]				
Length	71.5 ± 1.09	81.6 ± 2.21	74.5 ± 0.72	83.9 ± 1.14
Depth	16.9 ± 0.39	17.0 ± 0.89	17.0 ± 0.35	18.0 ± 0.47
Width	15.5 ± 0.21	14.6 ± 0.56	14.4 ± 0.38	15.2 ± 0.27
N	11	12	22	17

[a] Data for Sooty Oystercatchers come from the AMNH and the ROM. Data for Pied Oystercatchers come from Marchant and Higgins (1993).

[b] Bill lengths were significantly different for sexes within each species: Sooty, $F_{1,14} = 10.40$, $P < 0.01$ (this study); Pied, *t*-test, $P < 0.01$ (Marchant and Higgins 1993). See text for discussion of species differences.

[c] Data for both species comes from the AMNH and the ROM. The breakdown of the number of specimens for different states are as follows. Sooty male: Western Australia (1), New South Wales (2), Tasmania (8); Sooty female: Western Australia (2); New South Wales (1), Victoria (1), Tasmania (8); Pied male: Western Australia (4), Northern Territory (4), Queensland (3), Victoria (3), Tasmania (1), unknown (7); Pied female: Western Australia (5), Northern Territory (1), Queensland (4), New South Wales (2), unknown (5).

[d] Species, $F_{1,58} = 5.39$, $P < 0.05$; sex, $F_{1,58} = 13.45$, $P < 0.0001$; species × sex $F_{1,58} = 0.80$, $P > 0.05$ (NS).

DISCUSSION

This study documents a mechanism that segregates sympatric Pied and Sooty Oystercatchers foraging on mudflats adjacent to nesting areas at the Furneaux Islands, Australia. Our results showed that patterns of prey selection were generally consistent with that for other pied and black species of oystercatchers (Bent 1929, Heppleston 1972, Baker 1974, Hartwick 1974, Considine 1979, Hockey and Underhill 1984, Goss-Custard and Durell 1983, Nol 1984, Hayman et al. 1986, Hulscher and Ens 1992, Durell et al. 1993, Marchant and Higgins 1993) in that Sooty Oystercatchers captured higher proportions of hard prey and lesser proportions of soft prey when compared to Pied Oystercatchers. In addition, within each species males captured higher proportions of hard prey and lesser proportions of soft prey then females. However, our results suggest that bill length alone does not explain species differences in foraging behavior.

If bill size data which we present can be correctly applied to the birds we observed foraging, the results from our study contradict others regarding the relationship between foraging ecology and bill size for oystercatchers. If bill length alone predicted foraging behavior it would be

expected that Sooty Oystercatcher females, who had the longest bills, would capture more soft prey than hard prey when compared to Pied Oystercatcher females. Studies for other oystercatcher species have consistently shown that individuals with longer bills capture higher proportions of soft-bodied prey submerged in mud (Heppleston 1970, Swennen et al. 1983, Hockey and Underhill 1984, Hulscher 1985, Hulscher and Ens 1992, Durell et al. 1993). However, in our study Pied Oystercatcher females had a higher percentage of worms in their diet than Sooty Oystercatchers females.

Method of foraging (rapid or slow pecking) was invariably correlated with the type of prey captured (hard or soft-bodied) but was not always correlated with bill length. For those aspects of foraging behavior where we found significant differences, species differences were always stronger than the sex differences irrespective of bill length: males and females within a species were always more similar to each other in foraging behavior than the males or females of the two species were to each other. For example, time spent slow pecking for male and female Sooty Oystercatchers was more similar than the time spent slow pecking for males of each species. Thus, these results suggest that at the Furneaux Islands, species specific behavior was important in segregating the foraging roles of Pied and Sooty Oystercatchers.

Other evidence to suggest the importance of species specific differences in behavior to ecological segregation was that at foraging areas adjacent to nesting sites Sooty Oystercatchers fed at rocky shores as well as intertidal mudflats while Pied Oystercatchers utilized only intertidal mudflat for feeding (Lauro 1994). When nesting at rocky shores Sooty Oystercatchers fed primarily on the large intertidal limpet *Cellana solida* which they pried and hammered off rocks. Non-breeding Pied and Sooty Oystercatchers generally fed together in large groups (several hundred individuals) at intertidal mudflats adjacent to the western shore of Flinders Island (the main island of the Furneaux Group) and rarely fed at the available rocky coastline (Lauro, unpubl. data). Thus, Sooty Oystercatchers showed a dimorphism in feeding habitat choice and prey selection while Pied Oystercatchers showed no such dimorphism. A diet dimorphism related to habitat choice has also been documented during the breeding season for the European Oystercatcher (*Haematopus ostralegus*) (Safriel 1985)

Bill length is likely a better predictor for behavior and prey selection for sexes within species than between species. African Black Oystercatchers (*H. moquini*) at rocky shores have diet separation based on sexual dimorphism in bill size as males pried a greater proportion of limpets and whelks off rocks while females took more polychaete worms and small

unshelled prey (Hockey and Underhill 1984). Diet separation between the sexes in European Oystercatchers is similar, with females eating a higher percentage of soft-bodied prey (mainly worms) than males and employing different foraging techniques (Dare 1977, Swennen et al. 1983, Hulscher 1985, Hulscher and Ens 1992, Durell et al. 1993). In this species the difference was hypothesized to be due to similar differences in bill length and/or shape.

Three evolutionary hypotheses may explain sexual dimorphisms in bill morphology for birds in general (Shine 1989, Hedrick and Temeles 1989) and for oystercatchers specifically: (1) reduction of competition between males and females for limited resources (usually food), (2) partitioning of reproductive roles, or (3) sexual selection. These hypotheses explain in some combination the differences in foraging behavior and prey selection in our study. Consistent partitioning throughout the breeding season, both before and after the presence of chicks (Lauro, pers. obs.), and a lack of overt competition between the species in the non-breeding season (Nol, unpubl. data) lends some support to the hypothesis that the dimorphism functions to partition reproductive roles. Sexual selection is also likely to be important in explaining bill differences between oystercatcher sexes (Durell et al. 1993). The bills of oystercatchers are bright red and are used in ritualized breeding displays known as Piping (Hayman et al. 1986). Importantly, there is overlap in bill size for the sexes, yet within breeding pairs, males invariably have shorter bills than females, suggesting that there may be selection by sexes based upon bill length (Baker 1975, pers. obs.). The process of mutual sexual selection is likely involved (Jones and Hunter 1993). However, testing for this by either manipulation of bill coloration or bill length will be difficult in the oystercatchers because their long term pair bonds (Nol 1985) may preclude the opportunity to effectively quantify mate choice. Finally, bill shape in oystercatchers is somewhat plastic (Heppleston 1970, 1972; Swennen et al. 1983; Hulscher 1985) and future studies will be needed to determine the extent to which behavior and environment control the sexual dimorphism, as well species differences, in bill morphology.

ACKNOWLEDGMENTS

We thank Derek Smith, Garth Smith, Bobby Gardner, Duke Goss, and Margaret Goss for their assistance in the field at the Furneaux Islands. We are grateful to Allan Baker who suggested that Flinders would be a suitable site for field work and who suggested contacting Derek Smith. This work was funded by an NSERC (Canada) grant to E. Nol and Queen's Univ. Graduate Fellowships and Awards to B. Lauro. We appreciate the help of Barb Mountney in the preparation of the manuscript.

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GRADUATE AND POST-GRADUATE RESEARCH GRANTS

The Biological Research Station of the Edmund Niles Huyck Preserve offers grants (max. = $2500) to support biological research which utilizes the resources of the Preserve. Among the research areas supported are basic and applied ecology, animal behavior, systematics, evolution, and conservation. The 2000-acre Preserve is located on the Helderberg Plateau, 30 miles southwest of Albany. Habitats include northeast hardwood-hemlock forests, conifer plantations, old fields, permanent and intermittent streams, 10 and 100 acre lakes and several waterfalls. Facilities include a wet and dry lab, library, and houses/cabins for researchers. Deadline = February 1, 1996. Application material may be obtained from Dr. Richard L. Wyman, Executive Director, E.N. Huyck Preserve and Biological Research Station, P.O. Box 189, Rensselaerville, New York 12147.

Wilson Bull., 107(4), 1995, pp. 641–654

COMPARISON OF PHYLOGENIES DERIVED FROM TWO MOLECULAR DATA SETS IN THE AVIAN GENERA *PIPILO* AND *SPIZELLA*

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ABSTRACT.—We sequenced 433 bp of the mitochondrial DNA (mtDNA) cytochrome *b* (cyt *b*) gene from four species in the Brown Towhee complex (*Pipilo spp.*) and six species in the genus *Spizella.* Phylogenies derived from sequence data were compared to those derived from mtDNA restriction fragment length polymorphism (RFLP) data collected from the same individuals (Zink and Dittmann 1991, 1993), allozyme and sequence data were also combined. In *Spizella,* the sequence and RFLP data placed the American Tree Sparrow (*S. arborea*) basal and the Black-chinned and Field sparrows (*S. atrogularis* and *S. pusilla*) as sister taxa, but conflicted on the placement of Brewer's, Chipping, and Clay-colored sparrows (*S. breweri, S. passerina,* and *S. pallida*). Phylogenetic analysis of the combined sequence and RFLP data set for *Spizella* supports the two previously published hypotheses for the genus based on RFLP's alone (Zink and Dittmann 1993). Monophyly of *Spizella* including the American Tree Sparrow is supported. The *Pipilo* sequence tree was congruent with Zink and Dittmann's (1991) RFLP Dollo parsimony tree, suggesting that the White-throated Towhee (*P. albicollis*) is the basal member of the complex and not the sister-taxon to the Canyon Towhee (*P. fuscus*) as suggested by the RFLP Wagner parsimony tree and allozyme and morphometric data (Zink 1988). The *Pipilo* sequence and RFLP data agree in placing Abert's Towhee (*P. aberti*) as the nearest relative of the California Towhee (*P. crissalis*). Phylogenetic analysis of the combined data for *Pipilo* supports the basal position of the White-throated Towhee, but we still consider the position of this taxon unresolved. Overall, sequence and RFLP data produced significantly congruent phylogenetic trees in both genera, suggesting each type of data provides useful phylogenetic information. *Received 23 Nov. 1994, accepted 14 May 1995.*

Analyses of molecular data such as allozyme frequencies, restriction fragment length polymorphisms (RFLP's), and direct sequences of mitochondrial DNA (mtDNA) yield inferences about character evolution and phylogenetic relationships (Hillis et al. 1990, Avise 1994). These techniques, however, differ in their ability to resolve phylogenetic relationships along the taxonomic hierarchy (Avise 1986). Relatively few direct comparisons of phylogenetic patterns in different molecular data sets are available.

In studies of birds, phylogenetic trees derived from allozymes and mtDNA RFLP data were generally congruent (Zink and Avise 1990, Zink and Dittmann 1991). MtDNA, however, provided more characters for systematic analysis (Avise and Zink 1988). Direct sequencing of mtDNA

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may provide an enhanced view of molecular evolution and the evolutionary history of avian taxa because it reveals fine-scale patterns of variation not apparent in RFLP's (Edwards and Wilson 1990, Di Rienzo and Wilson 1991, Birt-Friesen et al. 1992, Edwards 1993). Our purpose was to compare phylogenetic trees derived from sequence data with those derived from RFLP data.

RFLP-based (restriction site and fragment) cladograms exist for four members of the Brown Towhee complex (Abert's Towhee [*Pipilo aberti*], White-throated Towhee [*P. albicollis*], California Towhee [*P. crissalis*], and Canyon Towhee [*P. fuscus*]) (Zink 1988, Zink and Dittmann 1991), and RFLP (restriction fragments only) cladograms exist for six members of the genus *Spizella* (American Tree Sparrow [*Spizella arborea*], Black-chinned Sparrow [*S. atrogularis*], Brewer's Sparrow [*S. breweri*], Clay-colored Sparrow [*S. pallida*], Chipping Sparrow [*S. passerina*], and Field Sparrow [*S. pusilla*]) (Zink and Dittmann 1993). We compared phylogenetic trees derived from cytochrome *b* (cyt *b*) sequence data with previously published trees (Zink and Dittmann 1991, 1993). We also combined the data sets to produce "total evidence" trees (Eernisse and Kluge 1993), to see if phylogenetic topologies were stable.

MATERIALS AND METHODS

The following specimens (general locality, voucher number [ARMZ = specimens with RMZ field catalogue numbers in the American Museum of Natural History, B = Louisiana State University], and Genbank accession number) were used: American Tree Sparrow (Alberta, B16372, U26190), Black-chinned Sparrow (California, B3859, U26191), Brewer's Sparrow (Arizona, B20007, U26192), Clay-colored Sparrow (Louisiana, B19765, U26198), Chipping Sparrow (California, B?; North Carolina, B?; Manitoba, B16505; Yukon, B18047, U26197), Field Sparrow (Texas, B15578, U26200), Abert's Towhee (Arizona, ARMZ2249, ARMZ2250; California, B14314, U26189), White-throated Towhee (Mexico, ARMZ2186, ARMZ2192, ARMZ2193, U26202), California Towhee (Baja California, ARMZ2159, ARMZ2160, U26193; California, B14334, B14336, B14351, ARMZ2396, U26194), Canyon Towhee (Arizona, ARMZ2373, ARMZ2375, U26195; Texas, B16731, B16733, U26196).

MtDNA was isolated from frozen tissues and purified in cesium chloride density equilibrium gradients following the protocols of Lansman et al. (1981), Avise and Zink (1988), and Dowling et al. (1990). MtDNA samples were the same as those used by Zink and Dittmann (1991, 1993). Purified mtDNA was amplified with the polymerase chain reaction (PCR) (Saiki et al. 1988). Symmetric amplifications were conducted in 30 ul reactions containing 0.625 units of *Thermus aquaticus* polymerase (Perkin-Elmer Cetus, Boehringer Mannheim), 1.25 mM $MgCl_2$, and dNTP's at a final concentration of 0.05 mM each. Primers L14841 (made by Operon; number refers to primer discussed in Kocher et al. (1989) and H15299 (Hackett 1992) were used at a concentration of 0.5 uM, and the concentrations of buffer components were 8.33 mM tris-HCL (pH 8.3) and 41.67 mM KCl. The thermal cycling regime consisted of an initial cycle of 3 min denaturation at 94°C, 1 min primer annealing at 50°C, and 1 min extension at 72°C. This was followed by 33 cycles of 1 minute each at 94°C, 55°C, and 72°C, and then a final extension of 10 min at 72°C. The presence and size of amplified product was verified by electrophoresis of 4 ul of reaction product

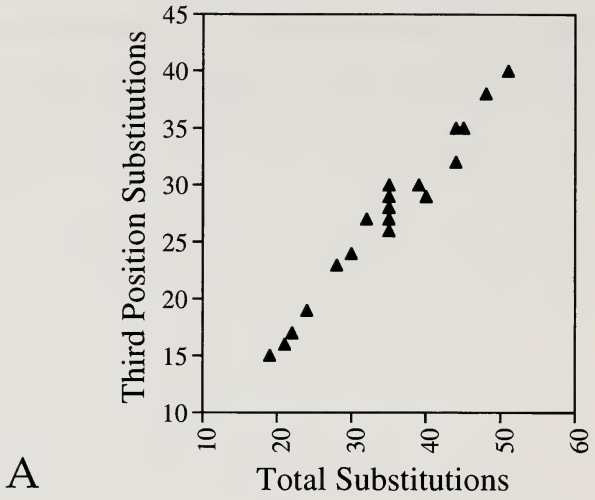
through a 1% agarose gel (SeaKem LE, FMC) in 1× TBE buffer. A 433 base-pair section was amplified from all samples.

The same primers were used to sequence the light and heavy strands of the amplified product using either a Silver Sequence kit (Promega), or a Sequenase PCR Product Sequencing Kit (United States Biochemical). Excess dNTP's and primers were removed from PCR product either by filtration (Millipore cat. no. UFC3 TTK 00) for silver sequencing, or by enzymatic treatment with Exonuclease I and Shrimp Alkaline Phosphatase (United States Biochemical) for Sequenase sequencing. Sequenced product was run through 0.4 mm, 6% polyacrylamide gels with a top buffer of either 0.8× or 1× TBE and a bottom buffer of 1× TBE. Glycerol-tolerant gels (with taurine-based buffer TTE) were also used. Sequences were visualized by silver staining (Silver Sequence, Promega; Caetano-Anolles and Gresshoff, 1993) or autoradiography (^{35}S), depending on the sequencing protocol used.

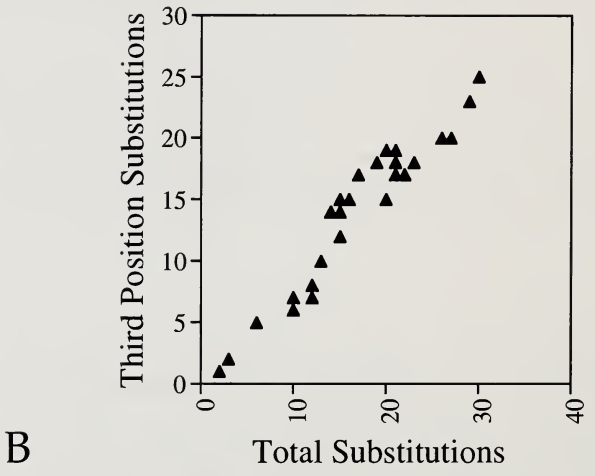
Sequences were read manually, and aligned to the sequence of the chicken (*Gallus gallus*) (Desjardins and Morais 1990). If conspecific sequences varied, each sequence was considered a separate haplotype. For *Pipilo,* a phylogenetic analysis that included all haplotypes was conducted to verify that all conspecifics grouped together. We computed statistics for nucleotide variation with the computer program MEGA (Kumar et al. 1993). Phylogenetic analyses of the sequence data were conducted using the computer programs PAUP 3.1.1 (Swofford 1993), Hennig86 (Farris 1988), and MEGA. All characters were analyzed as unordered. Dark-eyed Junco (*Junco hyemalis*) and Green-tailed Towhee (*Pipilo chlorurus*) (Genbank accession numbers U26199 and U26201, respectively) served as the outgroups for *Spizella* and the Brown Towhee complex. To test for the presence of phylogenetic signal in the sequence data sets, we used the computer program Random Cladistics (Siddall 1994) to conduct PTP tests (Faith and Cranston 1991) and used PAUP to obtain g_1 statistics. We used the nearest neighbor interchange (NNI) application of the computer program Component (Page 1993) to test whether phylogenetic topologies from different data sets were congruent. Phylogenetic analyses of data sets combining the sequence data with Zink and Dittmann's (1991, 1993) RFLP data were conducted using PAUP. To determine the level of support for nodes in particular tree topologies, PAUP was used to bootstrap (Felsenstein 1985) the sequence and combined data sets (1000 replications were conducted for each analysis).

RESULTS

Spizella.—Overall, the *Spizella* and *Junco* sequences varied at 85 of 433 sites, of which 33 were potentially phylogenetically informative (Appendix I). The four Chipping Sparrow specimens exhibited the same haplotype, despite the widespread sampling distribution. The variable nucleotide positions are distributed throughout the region sequenced and no insertions or deletions were noted. The distribution of variable sites by codon position is ten at the first position, six at the second position, and 69 at the third position. This variation resulted in 12 amino acid substitutions. The average transition:transversion ratio between the outgroup and ingroup in pair-wise comparisons was 3.96:1.00. A plot of total nucleotide substitutions vs substitutions at the third codon position in pairwise comparisons between ingroup taxa and the outgroup (Fig. 1A) showed a clear linear relationship, suggesting no saturation of substitu-



A



B

FIG. 1. A. Plot of total nucleotide substitutions vs third position substitutions in *Spizella*. B. Plot of total nucleotide substitutions vs third position substitutions in *Pipilo*.

tions (both transitions and transversions were considered together due to the low number of transversion events).

Tests for the presence of phylogenetic signal in the data set yielded conflicting results. The g_1 statistic for the *Spizella* sequence data indicated a significantly left-skewed distribution of tree lengths ($g_1 = -0.265623$),

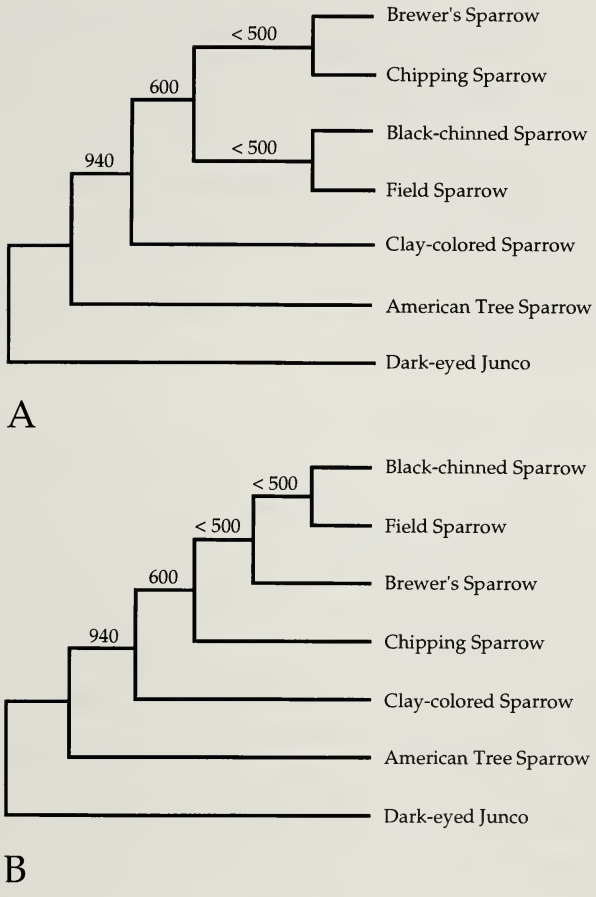
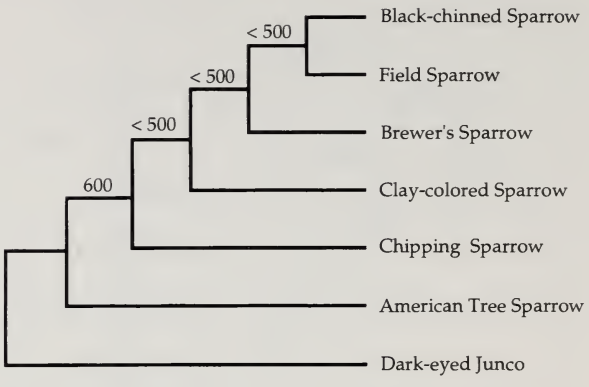


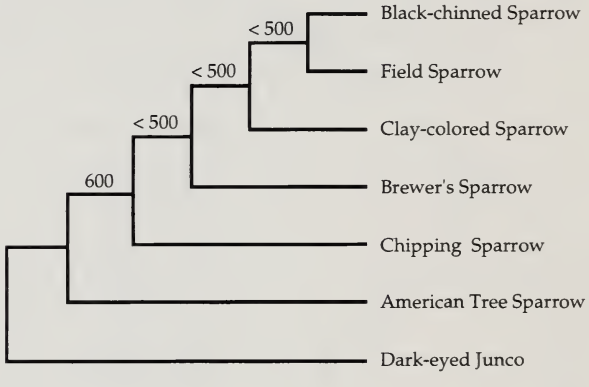
FIG. 2. The two equally most parsimonious trees from the exhaustive search of the *Spizella* sequence data (l = 122, ci = 0.762, ri = 0.396). Values at nodes refer to the number of times the node occurred in 1000 bootstrap replicates.

suggesting the presence of phylogenetic signal (Hillis 1991, Hillis and Huelsenbeck 1992). However, the PTP test of Faith and Cranston (1991) was not significant ($P = 0.1788$), indicating a lack of phylogenetic signal. We recognize that these tests are controversial (Carpenter 1992, Kallersjo et al. 1992).

The exhaustive search of the sequence data yielded two equally most-parsimonious trees (Fig. 2), which both show the Black-chinned and Field sparrows as sister taxa, the American Tree Sparrow as the most basal member of the ingroup, and the Chipping Sparrow as the second most basal ingroup taxon. The two trees differ in the position of the Brewer's



A



B

FIG. 3. The single best topology reported for RFLP data on *Spizella* (Zink and Dittmann 1993) derived from A = maximum parsimony, B = Fitch-Margoliash analyses. Analysis of combined RFLP and sequence data produced two equally most parsimonious trees (l = 366, ci = 0.525, ri = 0.377) with topologies identical to those of A and B. Values at nodes refer to the number of times the node occurred in 1000 bootstrap replicates of the combined data set.

and Clay-colored sparrows. The only relationship proposed by the sequence data that was supported in greater than 50% of bootstrap replicates was the clade containing all ingroup taxa except American Tree Sparrow.

An exhaustive search of the combined sequence and RFLP data yielded no novel phylogenetic hypotheses, as the two equally most-parsimonious trees feature the topologies of Zink and Dittmann's (1993) maximum parsimony and Fitch-Margoliash trees (Fig. 3). The bootstrap analysis of

the combined data strongly supports the basal positions of the American Tree and Clay-colored sparrows suggested by the RFLP data, but shows less than 50% support for relationships among the other four ingroup taxa (Fig. 3).

Pipilo.—The numbers of haplotypes for the *Pipilo* species were Abert's Towhee, 2; California Towhee (California), 3; California Towhee (Baja California), 2; Canyon Towhee (Arizona), 1; Canyon Towhee (Texas), 1; and White-throated Towhee, 1. Average haplotype divergence among conspecifics was: Canyon Towhee = 1.4% (between Texas and Arizona), California Towhee = 0.52% (including Baja California and California samples; there was no geographic variation), and Abert's Towhee = 0.15%.

A branch and bound search of all *Pipilo* haplotypes yielded two equally most-parsimonious trees (not shown) which differed only in that one tree did not show the Canyon Towhees from Texas and Arizona as sister taxa. Because all other conspecific haplotypes grouped together, taxa corresponding to those used by Zink and Dittmann (1991) (one Canyon Towhee from Arizona, one California Towhee each from California and Baja California, one Abert's Towhee, and one White-throated Towhee) were selected for direct comparison of the phylogenetic pattern from RFLP data. When conspecific haplotypes varied, the most complete sequence was chosen. The *Pipilo* sequences (including Green-tailed Towhee) varied at 46 sites, of which 27 were potentially phylogenetically informative (Appendix II). Variable nucleotide positions were distributed throughout the region of cyt *b* sequenced. The distribution of variable sites by codon position was six at the first position, three at second position, and 37 at third position, resulting in eight amino acid substitutions. The average transition:transversion ratio in pairwise comparisons between the outgroup and ingroup was 10.8:1.0. A plot of total nucleotide substitutions vs third position substitutions (transitions and transversions combined) (Fig. 2B) showed a clear linear relationship, suggesting no saturation of changes for observed transitions or transversions.

Tests for the presence of phylogenetic signal in the *Pipilo* sequence data set conflicted. Randomization tests (Faith and Cranston 1991) indicated no significant phylogenetic signal ($P = 0.1718$), whereas the g_1 statistic indicated a significantly left-skewed distribution of tree lengths ($g_1 = -0.349542$), suggesting the presence of phylogenetic signal (Hillis 1991, Hillis and Huelsenbeck 1992).

An exhaustive search of the selected haplotypes yielded a single most-parsimonious tree (Fig. 4) in which the California Towhees from California and Baja California were sister taxa, with Abert's Towhee, Canyon Towhee, and White-throated Towhee successively more basal. The boot-

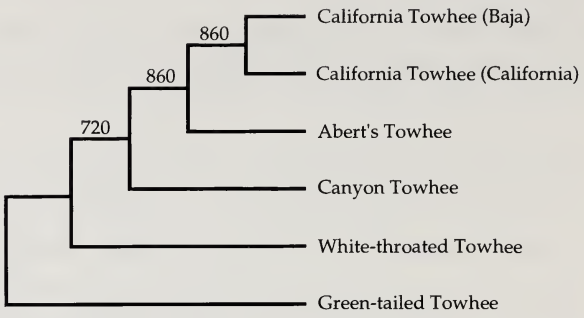


FIG. 4. Single most parsimonious tree (l = 51, ci = 0.824, ri = 0.625) from the exhaustive search of the *Pipilo* sequence data (also the topology of the RFLP Dollo parsimony tree [Zink and Dittmann 1991]). Values at nodes refer to the number of times the node occurred in 1000 bootstrap replicates.

strap of these haplotypes showed strong support for all nodes. Conducting the phylogenetic analysis with the Texas, instead of the Arizona, Canyon Towhee haplotype yielded a single tree of the same topology which is five steps longer (l = 56, ci = 0.839, ri = 0.640).

An exhaustive search of the combined sequence and RFLP data set yielded a single most-parsimonious tree (l = 241, ci = 0.900, ri = 0.750) which is congruent with the sequence data tree and Zink and Dittmann's (1991) Dollo parsimony tree (Fig. 4). All nodes were supported by at least 710 of 1000 bootstrap replicates.

DISCUSSION

RFLP's vs sequence data.—In phylogeny reconstruction, the phasing-out of restriction sites in favor of sequence data has been advocated (Wilson et al. 1989). However, because one is substituting single gene phylogeny estimates (sequence data) for an mtDNA genome-wide estimate (RFLP's), this may result in fewer informative characters in the sequence data set and a potentially less accurate phylogenetic estimate for the mtDNA genome (itself a single linkage unit). In both genera surveyed, the RFLP data sets contain more variable and phylogenetically informative characters (*Spizella:* 179 of 198 fragments variable, 67 informative; *Pipilo:* 98 of 119 sites variable, 77 informative) than the sequence data sets (*Spizella:* 85 of 433 nucleotides variable, 33 informative; *Pipilo:* 46 of 433 nucleotides variable, 27 informative). However, the cyt *b* sequence data provided information we could not have obtained from RFLP's (e.g. nucleotide substitutions by codon position), and one could sequence more DNA. The ci-values and tree lengths for RFLP and sequence data sets are not comparable owing to differing numbers of characters (Archie

1989). However, the ri-values, a measure of homoplasy that is not as influenced by the size of the data set, are similar for the two types of data (or higher for RFLP data), suggesting relatively equal amounts of "noise." Therefore, there are no obvious reasons to favor one data set over another based on these measures.

Several studies have found agreement between restriction site data and other evidence (Zink and Avise 1990, Dittmann and Zink 1991, Zink et al. 1991). In this study, the NNI tests (Page 1993) revealed that for both *Spizella* and *Pipilo,* sequence trees were significantly congruent (P = 0.0395) with the RFLP parsimony trees. The most likely reason for significant ($P < 0.05$) congruence is that each data set is "tracking" phylogeny. However, because the trees from each data set do not match exactly, further exploration of them is warranted.

In *Spizella,* one of the sequence trees (Fig. 2A) differs from the RFLP Fitch-Margoliash tree (Fig. 3B) only in the placement of the Clay-colored Sparrow and Chipping Sparrow. The other possible pairwise tree comparisons (Figs. 2, 3) differ by the placement of up to three taxa. For example, Fig. 2B and Fig. 3A agree only in the basal placement of the American Tree Sparrow and the sister-taxon relationship of Black-chinned Sparrow and Field Sparrow. Except for the basal position of the American Tree Sparrow, most suggested relationships do not exhibit high bootstrap values. Thus, if one were to compare only strongly supported nodes, there would be relatively few comparisons possible. However, the NNI tests suggested significant overall congruence, despite weak bootstrap support and topological differences, owing to the consistent basal placement of the American Tree Sparrow and the sister-group relationship between Black-chinned Sparrow and Field Sparrow. The relatively low ri values of the two data sets are similar (sequence ri = 0.40, RFLP ri = 0.42 [Zink and Dittmann 1993]), suggesting that character state changes are concentrated on terminal branches rather than on internal nodes (Farris 1989). This low "stemminess" is thought to decrease the probability that the correct topology has been found (Lanyon 1988, Rohlf et al. 1990). Phylogenetic resolution of the complete genus is not possible with either data set alone. It is likely that more data are required.

In *Pipilo,* the single most-parsimonious tree generated from the sequence data (Fig. 4) was topologically identical to Zink and Dittmann's (1991) Dollo parsimony tree. However, the sequence tree did not support the sister-taxon relationship between Canyon and White-throated towhees proposed by analysis of allozymes, morphometric data, and Wagner parsimony analysis of RFLP (sites or fragments) data (Zink 1988, Zink and Dittmann 1991). However, the two RFLP trees differ in length by only one step, and the sequence tree was significantly congruent (NNI, P =

0.0395) with the Wagner parsimony tree. The bootstrap analysis of the restriction site data supported the Canyon and White-throated towhees as sisters in 780 of 1000 replicates (Zink and Dittmann 1991), whereas the bootstrap of the sequence data supported the basal position of the White-throated Towhee in 710 of 1000 replicates. We conclude that the position of the White-throated Towhee is unresolved by both data sets.

We conclude that neither statistics associated with RFLP or sequence trees, nor the phylogenetic patterns themselves, favor one data set over the other for phylogenetic analysis.

Combined data and phylogenetic conclusions.—When two data sets conflict, some suggest that the best estimate of phylogeny is acquired by combining the data (Eernisse and Kluge 1993). We assumed the sequence and RFLP data sets were essentially independent because few restriction sites are likely to occur within a small region such as was sequenced. Maximum parsimony analysis of the *Spizella* combined data set showed the phylogenetic hypotheses proposed by the RFLP maximum parsimony and Fitch-Margoliash (Fig. 3) trees as equally most-parsimonious, although one of the trees from sequence data (Fig. 2B) was not favored by the combined data. The basal position of the American Tree Sparrow and the sister taxon relationship between the Black-chinned and Field sparrows were supported by all three data sets (sequence, RFLP, and combined). The combined data do not support the "*passerina*" complex, consisting of the Brewer's, Chipping, and Clay-colored sparrows, proposed by Mayr and Short (1970), which was also refuted by the RFLP data (Zink and Dittmann 1993).

The phylogenetic analysis of *Spizella* did not include the Worthen's or Timberline sparrows (*S. wortheni, S. taverni*), for which we lacked specimens. Worthen's Sparrow is assumed to be the sister taxon to the Field Sparrow (Mayr and Short 1970), and the Timberline Sparrow is assumed to be the sister taxon to the Brewer's Sparrow (Sibley and Monroe 1990). Inclusion of these putative terminal taxa in a phylogenetic analysis might help to clarify phylogenetic relationships by stabilizing internal nodes (Weller et al. 1992). Thus, we consider both tree topologies in Fig. 3 as working hypotheses.

We questioned the monophyly of *Spizella* because the sequence data showed that the average divergence from the American Tree Sparrow to other congeners is greater than that from the other congeners to the Dark-eyed Junco (0.0896); this result agrees with the RFLP data (Zink and Dittmann 1993). To test whether the American Tree Sparrow belongs in *Spizella* or to a separate clade, we added sequence data of additional taxa to the analysis (Green-tailed Towhee, White-throated Towhee, Black-throated Sparrow [*Amphispiza bilineata*], Fox Sparrow [*Passerella ilia-*

ca], Golden-crowned Sparrow [*Zonotrichia atricapilla*], and Song Sparrow [*Melospiza melodia*]). We varied the number of taxa, and used different combinations of taxa to root trees (results not shown). The American Tree Sparrow consistently appeared basal in *Spizella* when all additional taxa were included, regardless of which taxa were used to root trees. However, depending on which additional taxa we chose to include, the American Tree Sparrow would sometimes appear as the sister to the Chipping Sparrow, or as a member of a clade composed of one or more of the additional taxa. Mayr and Short (1970) suggested that the American Tree Sparrow has no close relatives, and molecular evidence indicates that this taxon may represent a long branch at the base of the *Spizella* clade, isolated by extinctions or differing rates of evolution. The occasional placement of the American Tree Sparrow outside *Spizella* may be due to one long branch attracting another (Felsenstein 1978). However, because of uncertainty over the correct outgroup(s) to use in addressing this question (Smith 1994), our test is not definitive. We conclude that present evidence favors monophyly of *Spizella* including the American Tree Sparrow.

Although the *Pipilo* sequence and RFLP data sets conflicted minimally the data sets were combined in hopes of gaining support for one hypothesis over the other. Phylogenetic analysis of the combined data also placed the White-throated Towhee as the most basal ingroup taxon and this node had strong bootstrap support (71%). However, placing the White-throated and Canyon towhees as sister taxa required only an additional three (1.2%) steps with the combined data. Green-tailed Towhee may not be an appropriate outgroup to resolve the placement of the White-throated towhee and conflict over the placement of this taxon may represent a rooting problem (Smith 1994). To test this, we added Collared Towhee (*Pipilo ocai*) sequence to our analysis. Rooting the sequence data tree with either Collared Towhee or both Green-tailed and Collared towhees, however, did not change the topology of the tree. More data are required to resolve the placement of the White-throated Towhee.

ACKNOWLEDGMENTS

We thank D. L. Dittmann for preparing mtDNA, and S. J. Hackett for providing us with the primer H15299 which she designed. A. Chubb, K. J. Johnson, J. T. Klicka, M. McGraw, and J. D. Weckstein provided helpful comments on this manuscript; K. W. Corbin and S. J. Weller reviewed an earlier version. This study was funded in part by a James W. Wilkie Fellowship awarded to AJF.

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Appendix I

Matrix of Phylogenetically Informative Characters in *Spizella*

Taxon	11111111222222233333344444 35567700134678035668923347790112 11813603265550553240584730918461 4
Dark-eyed Junco	GAGAGTATGAGCGTTGGGAAGGGGGCTGGCCTG
Chipping Sparrow	.GTGA.TGTGATACC..T.G.A...TC...T..
Black-chinned Sparrow	..T.AGTAAG.TA....C.G...AATCA.T.CA
Brewer's Sparrow	..TG.GTATGA.....TT...A.A..CA.TT..
Field Sparrow	..TGAGTGT.......TTG..A.A.TCA...CA
American Tree Sparrow	AG.....C.GAT.CCA...GA.A....AA.TC.
Clay-colored Sparrow	AGTG.GTGTG.....ATTG.AAA.A.CAATT.A

A "dot" indicates that the base is the same as that found in the Dark-eyed Junco. Numbers refer to the positions 1–433 in the region 15374 to 14941 corresponding to the chicken sequence (Desjardins and Morais 1990).

Appendix II

Matrix of Phylogenetically Informative Characters in *Pipilo*

Taxon	111111222333333 1122015668228447899 16928321060030390514
Green-tailed Towhee	?GAGCTGAATTGAAAGCAGA
Canyon Towhee	G..ATC....CA..G.TG.G
California Towhee (Baja)	A.G.TCAGGCC.GGGAT.AG
California Towhee (California)	A.GGTCAGGCCAGGGAT.AG
Abert's Towhee	A?GATCAGG..AG.GA...G
White-throated Towhee	GAG....GG.C..G..TG..

A "dot" indicates that the base is the same as that found in the Green-tailed Towhee. Numbers refer to the positions 1–433 in the region 15374 to 14941 corresponding to the chicken sequence (Desjardins and Morais 1990).

ERRATUM

In "The parasitic blow fly, *Protocalliphora spatulata,* in two new host species" by J.M. Fair and C.K. Miller (Wilson Bull. 107:179–181), all references to the scientific name *Protocalliphora hirundo* should be *P. hirudo.* Special thanks to Mia Revels for calling attention to this confusion between the similarity of the specific epithet *P. hirudo* and the specific epithet of a congener, *P. hirundo.*

Wilson Bull., 107(4), 1995, pp. 655–666

WITHIN-SEASON TRENDS IN THE FORAGING BEHAVIOR OF THE MOUNTAIN CHICKADEE

PAULA K. KLEINTJES[1,2] AND DONALD L. DAHLSTEN[1]

ABSTRACT.—We compared foraging behaviors of adult Mountain Chickadees (*Parus gambeli*) within and among breeding seasons. Foraging behaviors differed little between nestling and fledgling "feeding" periods of the breeding cycle with the exception of substrate use and foraging distance from the bole. During the nestling period birds spent the majority of foraging time searching for prey on the needles in the outer crown whereas during the fledgling period the birds spent significantly less time in the outer crown yet more time on new shoots. Among year variation was significant for the majority of foraging variables and data pooled for the entire breeding season masked within season trends. Our results indicate that within season comparisons of foraging behavior are important for revealing significant trends in behavior. They also suggest that Mountain Chickadees are opportunistic feeders and may time their breeding season with the growth of white fir so that older nestlings or fledglings are present when new shoots are expanded and thus contain a greater availability of prey to meet the demands of the older offspring. *Received 27 Jan. 1995, accepted 12 May 1995.*

Pooling foraging observations across the breeding season (Airola and Barrett 1985, Hill and Lein 1988, Grundel 1990) or into specific calendar months (Brennan 1989, Wagner 1981, Miles 1990) could fail to recognize minor, yet significant shifts in behavior associated with either the stages of the breeding cycle, nestling age, plant phenology or insect availability (Root 1967, Hejl and Verner 1990, Sakai and Noon 1990). In addition, among year comparisons are important because behavior may be influenced by annual weather patterns which affect plant phenology and insect availability and abundance as well as the onset and duration of the breeding season (Szaro et al. 1990, Dahlsten et al. 1992). The goal of our study was to observe whether the foraging behavior of Mountain Chickadees (*Parus gambeli*) differed between the nestling and fledgling "feeding" stages of the breeding cycle among years. Our specific objectives were to (1) determine the proportion of time Mountain Chickadees spend on each foraging location, substrate and tactic in white fir (*Abies concolor*) within the breeding season; (2) compare proportion of time spent on various locations, substrates and tactics within and between the two stages of feeding young (nestling, fledgling) during the breeding season each year and; (3) compare proportion of time spent on various locations, substrates and tactics during each stage among years.

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STUDY AREA AND METHODS

Our study area was in Modoc County in northeastern California (Dahlsten and Copper 1979, Dahlsten et al. 1992). The area is composed of white fir (60%) while the remaining 40% consists of ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), a naturally occurring Jeffrey X ponderosa pine hybrid, incense cedar (*Calocedrus decurrens*) and western juniper (*Juniperus occidentalis*) (Kleintjes 1993). Two 50 ha study plots, located 11.3 km apart, contain a total of 175 artificial nestboxes. There are 50 boxes at Toms' Creek (elev. 1675 m) and 125 at Yellowjacket Springs (elev. 1825 m). We used a color-banded population of breeding Mountain Chickadees that has been continuously monitored since 1965 (Dahlsten et al. 1992).

During the breeding seasons of 1990–1992, the breeding biology of the Mountain Chickadees was monitored from commencement of nestbuilding to the last day of fledging of second broods. Boxes were monitored 1–3 times a week in both plots. All data on nest condition, egg and nestling development and adult presence were also recorded. Breeding phenology was categorized according to calendar dates of egglaying/incubation, brooding and fledging of first broods, renests and second broods. We used a sequential observation technique with binoculars to record the foraging behaviors of adult Mountain Chickadees (Brennan and Morrison 1990). Each foraging observation (N = 1) consisted of a timed series of sequential records. At first sighting of a bird, a minimum of 10 seconds was allowed to pass (to avoid recording conspicuous behaviors). A series of sequential records was then recorded for a minimum of 20 to a maximum of 60 sec. Each record was equivalent to a set of variables which corresponded to the individual bird's foraging location, substrate and prey capturing maneuver (tactic). A new record (line of data) was made each time a bird changed foraging location, substrate or maneuver. New records were added to the observation until either the bird was lost from sight or the minimum time was reached. Each observation sequence was recorded on a tape recorder. The tape was rewound and each record timed according to a stopwatch and transcribed onto a data sheet. A minimum distance of 50 meters was moved between each observation to increase the likelihood of independence between observations made on the same day.

We used foraging variables modified from Remsen and Robinson (1990) to describe behaviors: tree species (white fir, Ponderosa pine, other); tree height (estimated to the nearest meter with a clinometer); bird height (in both meters and one-third crown intervals); horizontal location in tree (bole, inner, middle and outer one-third); foraging substrates on which activity occurred (needles, shoots, buds, air, small twigs, lichen, bark and other); time (for each record and total observation time); date; sex (if color band is visible). In addition, we recorded the tactic used to procure or attempt to procure prey. These included (1) searching (looking for prey-no predatory action); (2) perch gleaning (to pick food from a nearby substrate when in a perched position); (3) hang gleaning (to pick food from a nearby substrate while hanging upside down); (4) hover gleaning (to pick food from a nearby substrate while hovering in the air); (5) pecking (to drive bill against substrate to remove food); (6) probing (to insert bill into substrate to remove hidden food); (7) flycatching (to leave perch and aerially catch prey); (8) flaking (to pry bark and remove it to reach prey underneath); and (9) other. Foraging observations were collected during 1 June–15 July, 1990, 17 June–27 August, 1991 and 1 June–8 August, 1992. Foraging observations were recorded from both plots between 06:00–20:00 hr PST, 3–5 times per week while walking nestbox transect lines.

Raw data from each foraging observation were transformed from frequency of occurrence per observation to percentages of total observation time a bird used a specific location, substrate or tactic (Brennan and Morrison 1990). Conversion of the data to percent of total

observation time per individual transformed the data from discrete to continuous variables and assured independence of samples. Percentages were modified with a square root of the arcsin transformation because the range of percentages (for proportional data) did not lie between 30–70% (Sokal and Rohlf 1981).

A graphical procedure suggested by Morrison (1984) was used to determine the minimum number of observations needed to obtain appropriate estimates (stable means and variances) of behavior. We conducted the analysis on 1991 data for four variables that represented common use of substrate, tactic and location.

Means and variances for each variable of activity, location and tactic within the entire season for each year were compared using a standard one-way analysis of variance for equal sample sizes (Zar 1984). Pairwise comparisons of percent mean values were made with Tukeys HSD method (Zar 1984). Data were grouped into the two within breeding season stages that corresponded with feeding of young; nestling (brooding in cavity) and fledgling (post-brooding; outside of cavity). Since nestling development was not synchronous among nests (earliest and latest first broods varied by approximately 15 days), stage one ended during the week that first broods began to fledge. Therefore, stage two contained mostly fledglings with a few older first broods, renests and second broods in boxes. Means and variances for each variable of activity, location and tactic within and between breeding stages for each year were compared using a two-way factorial analysis of variance for proportional sample sizes (Zar 1984). We used Bonferroni-adjusted probability values (0.05/3 levels = $P < 0.016$) to adjust for the factorial design and variable degrees of freedom within each test. Separate ANOVA's were conducted on location level within crown, location distance from bole, foraging substrate and tactic. If significant interaction occurred between either period × level, period × substrate or period × tactic multiple comparison testing was used to seek significant differences between cell means (User-defined contrasts (UDC), Systat 1992).

Between year comparisons were made between equivalent breeding stages using a two-way factorial analysis of variance for proportional sample sizes ($P < 0.016$, Zar 1984). Separate tests were conducted on the same grouping of variables listed above. User-defined contrasts (UDC) were used for multiple comparison testing when the interaction between year × levels were significant. All statistical analyses were performed with Systat © 1992.

RESULTS

The breeding phenology of the Mountain Chickadee was nearly synchronous with the development of white fir shoots during all three years of the study despite the significant difference in phenologies among years (Table 1). Each year, white fir bud expansion occurred approximately one month after date of first egg and at this time in 1991 and 1992, the majority of nests contained nestlings 1–6 days old (Table 1). Of the three years, date of first laid egg was latest in 1991 (1 June) yet the latest date on record in 27 years at this site was 13 June (Dahlsten et al. 1992). Results of the sample size analysis indicated that the estimated means of various samples appeared to converge with the mean value for samples of a size $N > 40$. The standard deviations of the estimates stabilized within 50–60 observations so we chose a minimum sample size of fifty for appropriate estimates of behavior. Results were similar to those found by Brennan and Morrison (1990) for Mountain and Chestnut-backed

TABLE 1
BREEDING PHENOLOGY OF THE MOUNTAIN CHICKADEE, MAY–JULY 1990–1992, IN MODOC CO., CALIFORNIA

Measurement	1990	1991	1992
Date of first laid egg (DFE) of first broods	6 May	1 June	1 May
Date one month after DFE	10 June	1 July	1 June
Total number of first brood nests (N)	59	33	38
Percent of nests containing eggs	23%	6%	23%
Percent of nests containing nestlings 1–6 d old	35%	84%	68%
Percent of nests containing nestlings 7–12 d old	41%	9%	9%
Dates when >70% of first broods had fledged	18–25 June	13–18 July	10–17 June
Number of renests	4	2	4
Number of second broods	2	3	3
Dates of white fir bud expansion	15–22 June	25 June–2 July	3–10 June

chickadees in the Central Sierra Nevada. Birds were observed foraging on substrates other than white fir during all three years of the study. However, between 75–92% of the observations were recorded from white fir, therefore only these data were used for analysis.

The results indicated that during all three years, Mountain Chickadees spent a significantly greater proportion of their time foraging in the outer third of the crown (1990, $F = 7.87$; 1991, $F = 73.0$; 1992, $F = 78.9$; $P < 0.05$) (Fig. 1A). They also spent a significantly greater proportion (between 54–78%) of their foraging time searching for prey (1990, $F = 73.59$; 1991, $F = 199.58$; 1992, $F = 509.43$; $P < 0.05$) while perch gleaning and hang gleaning were the most common tactics used for obtaining prey (Fig. 1B). Only in 1991, did the birds spend significantly more time hang gleaning (18%) ($F = 199.58$, $P < 0.05$) (Fig. 1B). In 1990, the birds also spent a significantly greater proportion of time in the mid height crown level (47%) ($F = 7.87$, $P < 0.05$), whereas in 1991, they spent significantly more time on the middle (36%) and upper (40%) thirds of the crown ($F = 7.4$, $P < 0.05$) (Fig. 1C). Foraging on needles comprised the significantly greatest proportion of time spent on any given substrate in 1990 (57%) ($F = 61.68$, $P < 0.05$) and in 1991(45%) ($F = 65.6$, $P < 0.05$) (Fig. 1D). However, in 1992 birds spent nearly equal amounts of time on needles (36%) and shoots (33%) with both substrates being used significantly more than any others ($F = 62.81$, $P < 0.05$) (Fig. 1D).

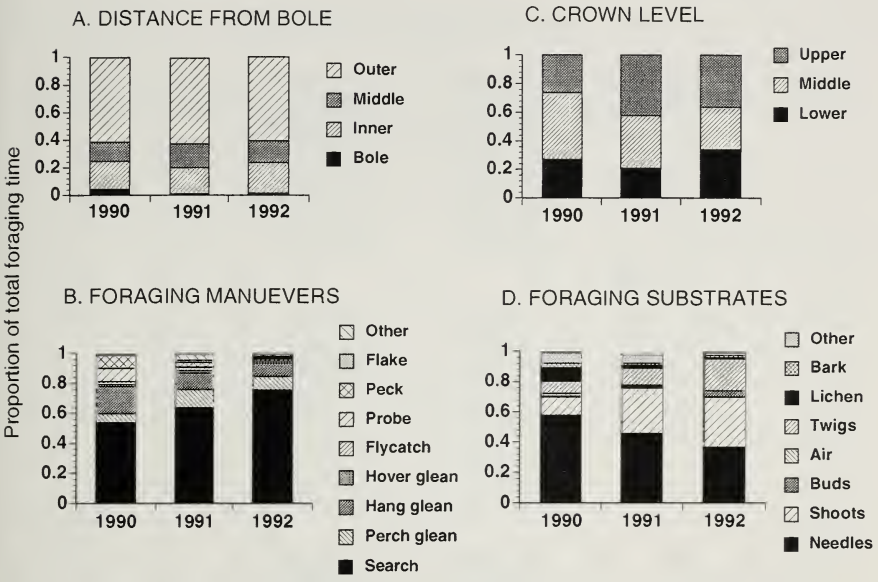

FIG. 1. Proportion of total observation time Mountain Chickadees spent on each foraging location, substrate and maneuver in white fir during the entire breeding season in Modoc Co., California, 1990–1992 (N = 120).

Within breeding season periods corresponded with 6–23 June (1st broods, stage 1) and 24 June–8 July (post-brooding, stage 2) in 1990, 18 June–13 July (stage 1) and 14 July–27 August (stage 2) in 1991 and 25 May–11 June (stage 1) and 15 June–8 August (stage 2) in 1992. Although statistical comparisons of behaviors produced variable results each year, two significant trends within the breeding season existed: an increased use of available shoots and an avoidance of the outer crown during the fledgling period. There were no significant differences in use of crown levels or foraging maneuvers between periods each year (Table 2).

Each year, the birds spent over 50% of their foraging time on older needles while feeding first broods. However, during period 2 (the stage of feeding older nestlings and fledglings) the birds significantly decreased their use of needles in exchange for more foraging time on new shoots (Table 2) (Fig. 2A–C). In 1992, use of shoots increased up to 57% during the fledgling period which was greater than any other substrate use (Table 2) (Fig. 2A–C). During the fledgling period of 1991 use of shoots only increased to (40%) and did not significantly differ from use of needles (30%), however, both needles and shoots were used significantly more than any other substrate ($P < 0.05$, UDC) (Fig. 2A–C).

During two of the three breeding seasons chickadees tended to avoid

TABLE 2

F VALUES AND SIGNIFICANCE LEVELS FROM TWO-FACTOR ANOVA'S USED TO TEST FOR SIGNIFICANT DIFFERENCES BETWEEN MOUNTAIN CHICKADEE FORAGING VARIABLES, PERIODS AND THEIR INTERACTION WITHIN EACH YEAR

	df	1990 *F* value	1991 *F* value	1992 *F* value
Crown height level				
Level	2	7.87[a]	7.40[a]	0.81
Period	1	0.00	0.02	0.00
Level × period	2	2.15	1.50	0.33
Distance from bole				
Distance	3	60.29[a]	73.00[a]	78.90[a]
Period	1	0.00	0.38	0.15
Distance × period	3	10.40[a]	6.10[a]	0.84
Substrate				
Substrate	7	61.68[a]	65.60[a]	62.81[a]
Period	1	0.04	0.01	0.09
Substrate × period	7	4.44[a]	10.37[a]	31.11[a]
Maneuver				
Maneuver	8	73.59[a]	199.58[a]	509.43[a]
Period	1	0.01	0.00	0.17
Maneuver × period	7	1.14	1.52	2.32

[a] $P < 0.016$ (Bonferroni-adjusted probability of $P < 0.05/3$), two-way ANOVA for proportional sample sizes.

foraging in the outer crown during the fledgling season and instead significantly increased their use of the bole and inner layers during 1990 and the middle layer in 1991 (Table 2, Fig. 3A–C).

The interaction between foraging variables and year within the nestling and fledgling period of the breeding season was significant for all groups of variables in both periods with the exception of crown height level during the fledgling period (Table 3). Each year birds spent the majority of their foraging time in the middle and upper crown levels. In contrast, during the 1990 nestling period, chickadees spent significantly more time (52%) in the midcrown than they did in 1992 (24%) (Table 3). Birds also spent significantly less time in the inner crown during 1990 than in either 1991 or 1992 (Table 3, Fig. 3A–C). Because bird height level significantly differed between years and not seasons we used a two sample *t*-test ($P < 0.05$) to compare between year differences (1991 and 1992) of the mean height (m) of birds and white fir. Data from 1990 was excluded due to measurement errors. The mean tree height (±SD) of white fir used by the birds was 15.8 m (±5.2) (N = 100) in 1991 and 16.3 m (±6.6)

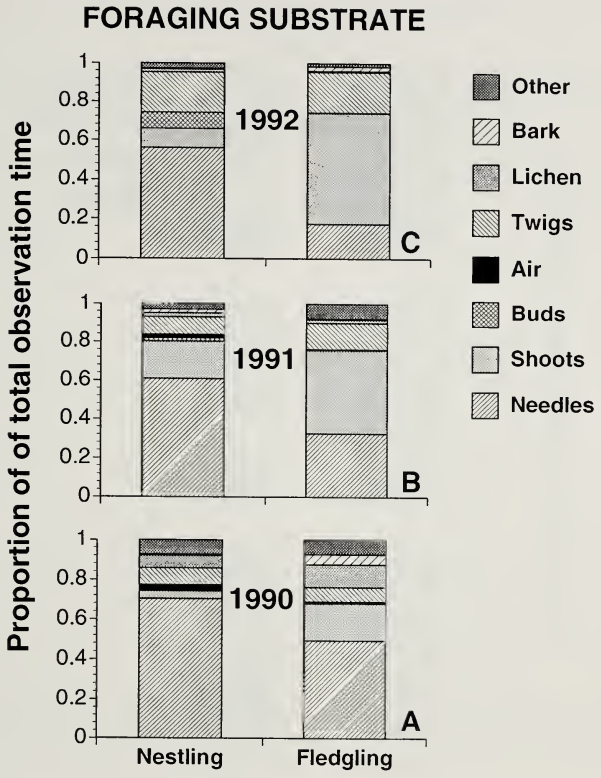

FIG. 2. Proportion of total observation time Mountain Chickadees used a foraging substrate of white fir during the nestling and fledgling "feeding" periods of the breeding season in Modoc Co., California, 1990–1992 (for each stage; N = 60, 1991–1992 and N = 54, 1990).

(N = 100) in 1992. Mean foraging height for birds was 10.0 m (±4.6) (N = 100) in 1991, and 9.8 m (±5.4) (N = 100) in 1992. Neither mean tree height nor foraging height significantly differed between years.

For the proportion of time spent on various foraging substrates, chickadees used shoots and twigs significantly more and needles significantly less during the 1992 fledgling period than they did in 1990 (Table 3, Fig. 2A–C). During the nestling period use of buds (8%) and small twigs (20%) was significantly greater in 1992 (Table 3, Fig. 2A–C). The most consistent, and not surprising trends in behavior across years for both feeding stages, was in chickadee foraging maneuvers. Birds spent the greatest percentage (50–70%) of time searching for prey, with hang gleaning and perch gleaning the most commonly used maneuvers for procuring

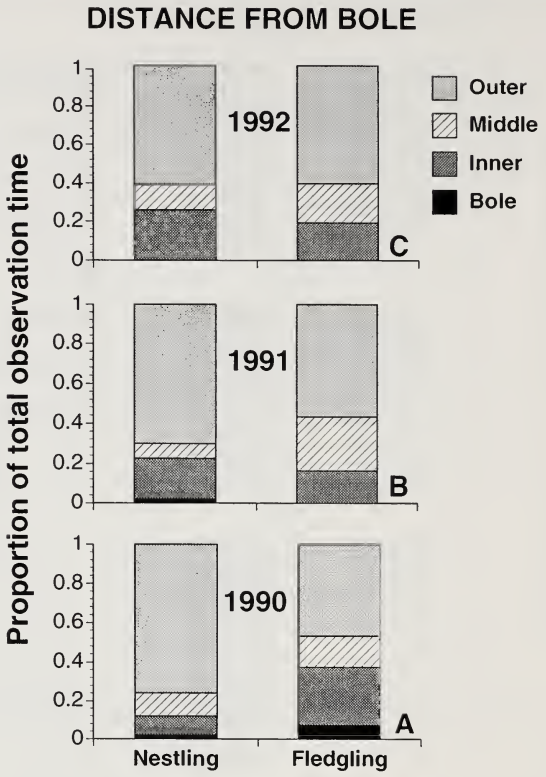

FIG. 3. Proportion of total observation time Mountain Chickadees spent foraging in the crown of white fir as a distance from the bole during the nestling and fledgling "feeding" periods of the breeding season in Modoc Co., California, 1990–1992 (for each stage; N = 60, 1991–1992 and N = 54, 1990).

prey. However, in 1990 the birds spent significantly less time perch gleaning compared to hang-gleaning (Table 3).

DISCUSSION

Our results found that Mountain Chickadees vary their foraging behavior both among and within breeding seasons. Among year variation was significant for the majority of variables whereas within breeding season behaviors varied little between the nestling and fledgling "feeding" periods with the exception of substrate use and foraging distance from the bole. This suggests that Mountain Chickadees may time their breeding season with the growth of white fir so that either older nestlings or fledglings are present when new shoots are expanded and thus contain a greater availability of prey to meet the demands of the older offspring. Brennan

TABLE 3

F VALUES AND SIGNIFICANCE LEVELS FROM ANOVA'S USED TO TEST FOR SIGNIFICANT DIFFERENCES BETWEEN MOUNTAIN CHICKADEE FORAGING VARIABLES, YEARS AND THEIR INTERACTION WITHIN "FEEDING" PERIODS

	df	Nestling period *F* value	Fledgling period *F* value
Crown height level			
Level	2	1.8	5.30[a]
Year	2	0.01	0.03
Level × year	4	4.34[a]	2.19
Distance from bole			
Distance	3	174.80[a]	68.79[a]
Year	2	0.63	0.26
Distance × year	6	2.81[a]	2.61[a]
Substrate			
Substrate	7	85.50[a]	67.3[a]
Year	2	73.90[a]	68.2[a]
Substrate × year	14	22.50[a]	19.1[a]
Maneuver			
Maneuver	7	249.05[a]	339.4[a]
Year	2	182.03[a]	207.5[a]
Maneuver × year	14	61.60[a]	83.87[a]

[a] $P < 0.016$ (Bonferroni-adjusted probability of $P < 0.05/3$), two-way ANOVA for proportional sample sizes.

(1989) also found within breeding season and among year variations in Mountain Chickadee foraging behavior, but these were in calendar month comparisons. In our study, we attributed within and among seasonal variation to annual differences in weather which in turn influenced plant phenology, breeding bird phenology and prey availability (see Kleintjes 1993). In addition, our significant within-season differences confirmed the importance of comparing stages of the breeding cycle, particularly since dates of the breeding season greatly differed among years.

Similar to Grundel and Dahlsten (1991) and Brennan (1989), we found that Mountain Chickadees spent the majority of their foraging time on white fir. In addition, the birds spent the majority of time on the outer crown. This was expected as the majority of prey found in the nestling diet were also found on the outer foliage (Grundel and Dahlsten 1991, Kleintjes 1993). Moreover, we examined differences in type of foliage used, i.e., needles, buds, and shoots. When data were pooled for the entire breeding season we found the birds spent the majority of their time on needles. In contrast, when data were compared between the "feeding"

stages, we found the birds spent a significantly greater amount of time on new shoots within the fledgling period. We attributed these differences to the availability of prey associated with the flush of new growth rather than a function of the fledgling stage. For example, insects such as *Acantholyda* sp. (Hymenoptera: Pamphiliidae) and *Choristoneura retiniana* (Lepidoptera: Tortricidae) were found both on the new growth of white fir and in the diet of nestling Mountain Chickadees (Grundel and Dahlsten 1991, Kleintjes 1993). The results are not surprising as Perrins (1991) found the breeding season of European *Parus* spp. to also coincide with the flush of new growth and availability of associated insect larvae.

The proportion of time the birds foraged in locations away from the bole also significantly differed between the nestling and fledgling stages of the breeding season. Although the birds still spent the greatest percentage (45–62%) of their time in the outer foliage compared to the inner canopy, they increased their use of the inner foliage during the fledgling periods of 1990 and 1991. Reasons for this change were likely a function of insect availability and more importantly, nestling age. It is known that after fledging birds often forage in family flocks and adults no longer need to watch for nest predators. Instead, adults spend more time attending fledglings in the protection of the inner canopy (Royama 1966). We often observed adult Mountain Chickadees feeding prey directly to fledglings resting on the inner branches. In 1990, birds spent a greater amount of time on the bole and inner canopy during the fledgling period than any other year which may have been due to the greater number of nests that fledged early in the breeding season.

Adult birds spent nearly equal amounts of time foraging in all three crown levels of white fir. This makes sense as proportions of selected prey differed little among the three crown levels (Kleintjes 1993). In contrast, Grundel (1984) found the birds spent the majority of their time in the upper crown, probably due to differences in insect availability and observation methods. Grundel repeatedly observed a limited number of specific breeding pairs for 30s intervals for extended periods of time whereas we collected 60s sequential observations on as many birds as possible throughout the season.

The percent of observation time spent on various foraging maneuvers was significantly different among years. The greatest amount of foraging time was spent searching whereas foliage gleaning maneuvers, typical of the Paridae, were the second most common use of time. Minor annual differences in proportions of various maneuvers were most likely due to changes in availability and abundance of different prey items, i.e., gleaning Lepidoptera and Hymenoptera larvae from shoots vs. flycatching adult moths from the air.

Our data indicate that Mountain Chickadees will vary their foraging behavior both within and among breeding seasons. Such plasticity in behavior allows adult Mountain Chickadees to exploit prey availability on white fir throughout the breeding season for feeding both nestlings and fledglings. This work also illustrates that within season comparisons of foraging behavior associated with feeding stages of the breeding cycle avoid masking differences in behavior that may result from pooling data into calendar months, an entire breeding season or years.

ACKNOWLEDGMENTS

We thank R. Garcia and M. L. Morrison for reviewing earlier versions of this paper and L. A. Brennan for helpful advice and suggestions. We also extend our appreciation to W. C. Copper, D. L. Rowney, E. C. Roswall, D. Su and S. Hug for their technical assistance in the field.

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Wilson Bull., 107(4), 1995, pp. 667–674

DEMOGRAPHICS OF A DECLINING FLOCK OF GREATER SANDHILL CRANES IN OREGON

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Abstract.—Greater Sandhill Crane (*Grus canadensis tabida*) nesting success at Malheur National Wildlife Refuge, Harney County, Oregon, was 44% for 456 nests during 1966–1974, and increased to 54% for 640 additional nests during 1976–1989. Predators destroyed 241 (38%) clutches in the 1976–1989 period, with Common Ravens (*Corvus corax*) taking 63, raccoons (*Procyon lotor*) 43, coyotes (*Canis latrans*) 28, and unknown predators 107. Most clutches lost to unknown predators were likely destroyed by coyotes. A total of 52 clutches was either abandoned, flooded, or infertile. The mean annual number of fledged young from 1970–1989 was 31, and mean annual young mortality from hatching to fledging was 84.4%. Of young fledged, a total of 438 broods contained one young and 91 had two ($\bar{x}$ = 1.14). The 6.7% mean annual recruitment at Malheur between 1970–1989 probably was responsible for a decline in breeding pairs, from 236 in 1975 to 168 in 1989. *Received 17 Jan. 1995, accepted 15 May 1995.*

Malheur National Wildlife Refuge, Harney County, Oregon (Malheur) is an important Greater Sandhill Crane (*Grus canadensis tabida*) nesting area. Cranes nesting at Malheur are affiliated with the Central Valley Population (CVP) (Braun et al. 1975). An interspersion of meadow-marsh and shrub-covered uplands provide excellent crane production habitat for about 200 pairs (Littlefield and Thompson 1979, Littlefield et al. 1994). Between 1977 and 1989, breeding pairs declined, resulting in a predator management program being initiated in 1986. The principle predators on eggs and prefledged young, coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and Common Ravens (*Corvus corax*) were removed by trapping, toxicants (DRC 1339 for raven control), and shooting (Ivey 1990).

I studied crane productivity at Malheur from 1966–1989. Findings from 1966–1967 were presented by Littlefield and Ryder (1968) and 1968–1974 by Littlefield (1976). The objective of this study is to report annual reproduction in Greater Sandhill Cranes (greaters) nesting at Malheur from 1976–1989 and compare findings with earlier results (1966–1974).

STUDY AREA AND METHODS

Malheur Refuge is in the semi-arid northern Great Basin of southeastern Oregon. Upland vegetation there consists of low shrubs dominated by big sagebrush (*Artemisia tridentata*). The landscape has internal drainage systems and large wetland complexes occur, with one of the largest being the Malheur-Harney Lakes Basin, where Malheur is located. About 12,200 ha of crane breeding habitat occurs within this 75,117 ha refuge. Normally in August,

[1] Malheur Field Station, HC 72 Box 260, Princeton, Oregon 97721. (Present address: HCR 4 Box 212, Muleshoe, Texas 79347).

TABLE 1

GREATER SANDHILL CRANE CLUTCH SIZES FOR 19 YEARS BETWEEN 1966–1989, AT MALHEUR NATIONAL WILDLIFE REFUGE, OREGON

Year	N	Clutch size				$\bar{x}$ clutch size
		1	2	3	4	
1966	52	4	48	—	—	1.92
1967	56	5	51	—	—	1.91
1969	80	3	77	—	—	1.96
1970	67	2	65	—	—	1.97
1971	74	6	68	—	—	1.92
1973	35	4	31	—	—	1.89
1974	33	—	32	1	—	2.03
1976	74	2	72	—	—	1.97
1977	37	6	31	—	—	1.84
1978	41	5	36	—	—	1.88
1980	28	3	25	—	—	1.89
1981	42	7	35	—	—	1.83
1982	71	7	63	1	—	1.92
1983	62	8	53	—	1	1.90
1984	48	5	42	1	—	1.92
1985	32	1	31	—	—	1.97
1986	60	9	51	—	—	1.85
1987	46	4	42	—	—	1.91
1989	36	3	33	—	—	1.92
Total	974	84	886	3	1	1.92 (0.05)[a]

[a] (SD).

most cranes begin congregating at several barley fields and remain until they migrate to California wintering areas in October and November (Littlefield 1992). Detailed descriptions of Malheur are provided by Littlefield (1990).

Pairs were counted in 1970, 1975, 1978, 1980, 1982, 1985, 1986, and 1989 in March and April. Breeding territories were surveyed until pairs were located or were determined to be missing. I searched for nests in April and May. After a 30-day incubation period, nests were revisited and fates assessed.

Using a 20× spotting scope, I counted fledged broods on refuge grain fields from a vehicle in September before autumn cranes arrived. However, in the western portion of the refuge, pairs often remained in mowed hay meadows, and they were counted in late September from aircraft.

Recruitment is expressed as (number fledged young/fledged young + breeding adults) × 100. Long-term means reported were weighted by year. I used a *t*-test to compare fledging success (young/pairs) for years with and without predator control.

RESULTS

During 19 years between 1966–1989, mean clutch size was 1.92 (Table 1). For 974 completed clutches, 84 (8.6%) contained one egg, 886

TABLE 2

GREATER SANDHILL CRANE NEST FATES AT MALHEUR NATIONAL WILDLIFE, OREGON, 1976–1989 (PERCENTAGE IN PARENTHESES)

		Nest fate					Nests lost to predators			
Year	N	Hatched	Aband.	Flooded	Infert.	Predated	Raven	Raccoon	Coyote	Unk. pred.
1976	52	35 (67)	0	0	1 (2)	16 (31)	4	6	0	6
1977	50	23 (46)	0	0	1 (2)	26 (52)	9	6	3	8
1978	55	19 (34)	1 (2)	10 (18)	1 (2)	24 (44)	7	5	5	7
1980	30	16 (53)	1 (3)	2 (7)	0	11 (37)	4	2	1	4
1981	31	15 (48)	0	0	2 (7)	14 (45)	5	2	0	7
1982[a]	81	54 (67)	2 (2)	0	1 (1)	24 (30)	8	2	3	11
1983[a]	61	38 (62)	3 (5)	3 (5)	1 (2)	16 (26)	2	5	5	4
1984	67	23 (34)	2 (3)	5 (7)	3 (5)	34 (51)	8	5	8	13
1985	50	24 (48)	1 (2)	0	0	25 (50)	7	1	0	17
1986[a]	60	40 (67)	2 (3)	0	2 (3)	16 (27)	2	2	1	11
1987[a]	61	35 (57)	2 (3)	0	3 (5)	21 (34)	4	4	0	13
1989[a]	42	25 (60)	2 (5)	0	1 (2)	14 (33)	3	3	2	6
Total	640	347 (54)	16 (2)	20 (3)	16 (2)	241 (38)	63	43	28	107

[a] Predator management programs in progress.

(91.0%) two eggs, 3 (0.3%) three eggs, and one clutch contained four eggs (0.1%) (Littlefield and Holloway 1987). Nest success for 456 clutches was 44% during 1966–1974 (Littlefield 1976). For 1976–1989 (excluding 1979 and 1988), 640 additional nests were examined and 347 (54%) hatched at least one egg (Table 2). Lowest nesting success was in 1978 and 1984 with 34%, and the highest success was 67% in 1976, 1982, and 1986.

Predators destroyed 241 (38%) clutches, including 63 by Common Ravens, 43 by raccoons, 28 by coyotes, and 107 by unknown predators (Table 2). Coyotes usually removed eggs and ate them at drier sites, leaving little or no evidence at nests. Most clutches lost to unknown predators were likely destroyed by coyotes. Predated nests annually ranged from 26% (1983) to 52% (1977). Other lost clutches included 16 abandoned (2%), 20 flooded (3%), and 16 contained infertile eggs (2%). Fertility rate for 711 eggs was 93.1%.

The mean number of young fledged annually from 1970–1989 was 31. With intensive predator control, 68, 46, 50, and 43 young fledged in 1970, 1971, 1986, and 1987, respectively. Largest numbers fledged in non-predator control years were 43, 47, and 43 in 1972, 1976, and 1978, respectively, and the fewest young fledged was two in 1973 and 1974 (Table

3). Fledging success was higher in years with predator control than in years without control ($t = -2.56$, df = 18, $P < 0.05$).

Average mortality from hatching to fledging was 84.4%, ranging from 66.5% (1970) to 98.8% (1974). Lower mortality was recorded in 1978 (70.1%), and in years with intensive predator control (1986—77.6%; 1987—78.4%; 1989—74.7%). Annual recruitment averaged 6.7% for 1970–1989 (Table 3). Lowest recruitment rates were in 1973 and 1974 (0.4%), 1975 (3.5%), 1985 (2.4%), and 1988 (1.6%); highest recruitment was in years with predator control, including 1970 (12.6%), 1986 (12.1%), and 1989 (12.7%). A total of 438 broods with 1 young and 91 broods with 2 young fledged ($\bar{x} = 1.14$) between 1970–1989; no broods with 3 or 4 young fledged.

DISCUSSION

Mean clutch size at Malheur is generally similar to the 1.96 eggs per clutch reported for cranes in Michigan (Walkinshaw 1973), 1.94 in Idaho (Drewien 1973), 1.91 in Wisconsin (Bennett 1978), and 1.91 in California (Littlefield 1995). Below average annual clutch sizes occurred at Malheur in 1973 and 1977 when severe drought conditions prevailed; however, in four other years, clutch sizes <1.90 occurred without obvious explanation.

Crane nesting success at Malheur was mainly below those reported elsewhere within the subspecies range. In Michigan, nesting success ranged from 77 to 78.9% (Hoffman 1979, Walkinshaw 1981), 78% in Idaho (Drewien 1973), and 84% in Wisconsin (Bennett 1978). However, nesting success was higher than 44% recorded from earlier Malheur studies (Littlefield 1976) and 29.8% success at Sycan Marsh, Oregon (Stern et al. 1987).

Improved nesting success (54%) at Malheur during 1976–1989 was attributable to improved nesting habitat. Between 1974–1983, cattle, which had excessively winter-grazed Malheur wetlands, were substantially reduced in numbers (Littlefield and Thompson 1987), providing residual vegetation for increased nest concealment. Although habitat improvement increased crane nesting success (Littlefield and Paullin 1990), brood survival generally declined and recruitment was <10% except for most years with predator control (Table 3). In 1972, toxicants (primarily Compound 1080) used for coyote control were banned on federal lands, and coyotes increased dramatically in southeastern Oregon (Willis et al. 1993). Radio-telemetry studies on flightless crane chicks at Malheur in the early 1980s showed that coyote predation was primarily responsible for low fledging success (Littlefield and Lindstedt 1992).

The 6.7% mean recruitment at Malheur between 1970–1989 was below

TABLE 3

BREEDING PAIRS, PERCENT MORTALITY OF YOUNG FROM HATCHING TO FLEDGING, NUMBER OF FLEDGED YOUNG, AND RECRUITMENT OF GREATER SANDHILL CRANES AT MALHEUR NATIONAL WILDLIFE REFUGE, OREGON, 1970–1989

Year	Breeding pairs	No. fledged young	Percent young mortality	Percent recruitment[a]
1970[b]	235	68	66.5	12.6
1971[b]	235	46	80.7	8.9
1972	235	43	ND	8.4
1973	235	2	98.0	0.4
1974	235	2	98.8	0.4
1975	236	17	ND	3.5
1976	236	47	84.6	9.1
1977	236	27	85.5	5.4
1978	219	43	70.1	8.9
1979	219	39	ND	8.2
1980	221	34	84.9	7.1
1981	221	23	88.7	5.0
1982[b]	214	25	90.1	5.5
1983[b]	214	39	84.8	8.4
1984	214	8	93.9	1.8
1985	186	9	92.6	2.4
1986[b]	181	50	77.6	12.1
1987[b]	181	43	78.4	10.6
1988[b]	181	6	ND	1.6
1989[b]	168	49	74.7	12.7
$\bar{x}$ (SD)	215 (22.9)	31 (18.8)	84.4 (9.4)	6.7 (4.0)

[a] Recruitment = (no. young fledged/young fledged + no. breeding adults) × 100.
[b] Predator management programs in progress.

desired levels. I attribute low recruitment as being primarily responsible for the declining number of nesting pairs at Malheur (Table 3). In 1970, 235 pairs occupied breeding territories and 236 in 1975. Low recruitment began in 1973, but a decline in nesting pairs was not detected until 1978. From 1978–1981, 219–221 pairs occupied territories, but pairs continued to decline in the mid-1980s and by 1985 had decreased to 186, with only 168 pairs present in 1989 at the end of the study.

Low recruitment (4.5%) was reported for cranes at Sycan Marsh, Oregon (Stern et al. 1987), and for the entire CVP of Greater Sandhill Cranes (5.6–6.1%). This is one of the lowest rates recorded for North American cranes (Drewien et al. 1995). Greater Sandhill Cranes nesting in the Great Lakes region (eastern population) have been increasing, and recruitment rates have averaged 12–12.7% (Lovvorn and Kirkpatrick 1982, Drewien et al. 1995), while cranes breeding in the Rocky Mountain

states (Rocky Mountain population) ranged from 9.4 to 12% in the early 1970's (Drewien et al. 1995) and the population was increasing during this period. Since 1986, recruitment has declined, ranging from 3.4 to 6.5%. Presently, this population is stable or slightly decreasing (Drewien et al. 1995).

Even though other mortality factors are prevalent within the CVP nesting in Oregon and California, the most important population limitation appears to be low annual recruitment. With high predation on eggs by Common Ravens, raccoons, and coyotes, and losses of young to coyotes, few young fledge. Only in years with predator control have recruitment rates exceeded those apparently necessary for population stability at Malheur.

Due to longevity and deferred breeding age of adult Greater Sandhill Cranes (Drewien et al. 1995), a decline in breeding pairs at Malheur did not occur for a number of years. Although recruitment was extremely low in 1973 and 1974, nesting pairs continued to increase through 1975 and remained stable through 1977, followed by a slight decline and again general stability through 1982 (Table 3). With attrition of older breeders, pairs dropped abruptly in 1985, 12 years after declining recruitment was first recorded. This indicates that caution is warranted when an increased mortality factor is introduced into a sandhill crane population, as it may take a number of years before higher mortality results in a decrease in breeding adults.

A predator management program at Malheur was initiated in 1986 to curtail the accelerated decline in breeding pairs. Excluding the severe drought year of 1988, recruitment increased during control years. By 1993, the Malheur breeding population had rebounded to 230 pairs after 8 years of predator control (Ivey 1993).

Because of long-term annual monitoring of the nesting crane population at Malheur, corrective measures were undertaken to reduce predation on eggs and young. Had an annual monitoring program not been in progress, it would likely have been several additional years before the decline was detected and corrective measures initiated. The U.S. Fish and Wildlife Service continues to annually monitor breeding pairs and reproduction, and if new problems are detected corrective management actions will be initiated (G. L. Ivey, pers. comm.). Due to predator control, breeding pairs in 1993 are presently near the peak number (236) recorded in 1975.

ACKNOWLEDGMENTS

The study was funded by the U.S. Fish and Wildlife Service. I especially thank J. E. Cornely, B. D. Ehlers, G. L. Ivey, S. P. Thompson, and other Malheur refuge employees who participated in the field work. Refuge managers J. C. Scharff and J. Mazzoni provided

time and support during the study, and H. F. Duebbert, D. B. Marshall, and R. A. Ryder were instrumental in first initiating crane studies on Malheur in the 1960s. I thank R. C. Drewien for information and comments on several drafts of the manuscript and S. H. Boufford for assistance with statistical analysis.

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Wilson Bull., 107(4), 1995, pp. 675–685

BREEDING BIOLOGY OF A GREY EAGLE-BUZZARD POPULATION IN PATAGONIA

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Abstract.—We studied the breeding performance of a Grey Eagle-Buzzard (*Geranoaetus melanoleucus*) population in a region of northern Argentinian Patagonia where two different habitats occur; the mountains near the Andean cordillera and the plains where shrub-steppes predominate. Mean eagle density was 1 pair/19 km² (N = 44), with higher densities occuring in the plains (1 pair/13.2 km², N = 17) than in the mountains (1 pair/22.7 km², N = 27). We located four communal roosts, with a maximum number of 14 immature birds roosting together. Of 1254 prey items identified from pellets, most were European hares (*Lepus europaeus*) (58.2%), rodents (19.1%), and birds (16.5%). Diet varied between pairs and between those breeding in the mountains and those in the plains. The number of nests per pair was significantly higher in the plains (5.1 nests/pair, N = 9 pairs) than in the mountains (3.2 nests/pair, N = 14 pairs). Breeding success was similar in both breeding seasons. About 80% of the pairs laid eggs and over 60% successfully raised at least one young. The number of fledgling young per pair varied between one and three. The mean number of fledglings per successful pair was 1.8. The values of breeding density and success are the highest published for this species (and among the highest for other large eagles), probably because the species exploits the abundant European hare, a mammal introduced to Patagonia at the beginning of the century. *Received 12 Sept. 1994, accepted 10 May 1995.*

The Grey Eagle-Buzzard (*Geranoaetus melanoleucus*) is the largest Buteoninae, weighing 1670–3170 g (Jiménez and Jaksic 1990). Its range extends from Venezuela to Tierra del Fuego. It prefers open country with steep landscapes. It is seen more rarely in the plains (Brown and Amadon 1968, Jiménez and Jaksic 1990). In Patagonia the Grey Eagle-Buzzard is the largest raptor species, except for Cathartidae, and the birds are relatively undisturbed by man (Donázar et al. 1993). The most significant recent change in the ecology of this region has been the introduction of two lagomorph species: the European hare (*Lepus europaeus*)—introduced in 1888 in central Argentina (Godoy 1963) and around the beginning of this century in our study area (authors unpubl.)—and the European rabbit (*Oryctolagus cuniculus*) that recently (1945–1950) expanded its range across the Argentinian border from Chile (Howard and Amaya 1975). There are few studies on the Grey Eagle-Buzzard, and none have provided quantitative data (see review in Jiménez and Jaksic 1990). Food

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habits of Grey Eagle-buzzards have been reported for some Chilean sites (Schlatter et al. 1980; Jiménez and Jaksic 1989, 1990; Iriarte et al. 1990), but based on few prey items (only one study with more than 100 prey). The breeding biology is almost unknown. There are few records of nest site characteristics and reproductive parameters (see review in Jiménez and Jaksic 1990).

This study provides measurements of population density, feeding habits, and reproductive parameters for a Grey Eagle-Buzzard population occupying a relatively undisturbed area in northern Argentinean Patagonia. Information on nest-site location and orientation has been published elsewhere (Travaini et al. 1994). We compare our results with population parameters from other large eagle populations in regions (mainly Europe) comparatively more disturbed by human activities.

STUDY AREA AND METHODS

We performed this study in the Province of Neuquén, northern Patagonia, Argentina, in a circle of 60–70 km radius centered at the town of Junín de los Andes (39°57′S and 71°05′W, 780 m above sea level). The study area contained two distinct physiographic areas: mountains and plains. The mountains (spurs of the Andean range) occupy the northern and western portions of the study area, with the highest peaks reaching 1600 m. The plains are located in the southeastern part of the study area and are dissected by steep valleys. The weather is cold and dry with a pronounced gradient of rainfall from the mountains (800 mm average annual rainfall) to the plains (300 mm). The area belongs to the Patagonian phytogeographic province, Western District (Cabrera 1976). The vegetation is typically mixed grass and shrubs. Dominant species are *Mullinum spinosum, Senecio* spp., *Stipa* spp., and *Poa* sp. Some of the common woody shrubs are *Chacaya trinervis, Berberis darwinii,* and *Schinus molle.* In the bottom of the valleys there are marsh zones, called "mallines", with dense herbaceous vegetation, where dominant species are *Cortadeira araucana, Juncus* spp., and *Carex* sp. Woody species such as *Maytenus boaria* and *Salix humboldtiana* are frequent in valleys and near mallines, particularly in the mountains.

We conducted this study during the spring and summer (September–February) of two consecutive breeding seasons, 1991–92 and 1992–93. Grey Eagle-Buzzard territories were located by means of personal inquiries to land owners and ranch workers, active searches in a vehicle along main and secondary roads, and cross-country searches on foot. We used binoculars (10 × 40) and spotting scopes (20 to 40×) to check cliffs and other potential nesting sites. The more thorough censuses were done along the valleys of the main rivers, due to the higher density of roads in those places. Roosting sites of juveniles were located by observing juveniles' activity late in the afternoon. During the autumn of 1993 (May) the whole area was searched again to check the status of territories and roosts.

Food habits of breeding eagles were analyzed by using pellets collected throughout the breeding season below nests and perches within territories. Pellets were dried, and their contents were separated. Osseous remains were identified to the lowest taxonomic level possible, using a reference collections (i.e., birds, small mammals) and small mammal skull keys (Pearson 1986). Mammal hair was identified through medula types and scale patterns following the methodology of Brunner and Coman (1974) and the keys of Chehébar and Martin (1989). Each species found in a pellet was considered as one prey item unless there was clear evidence of more than one individual. Biomass contribution of prey items was

not calculated. We compared the contents of pellets collected during incubation and the first half of the nestling period (from adult birds only) with pellets collected during the second half of the nestling period and postfledging period (from adult birds and fledged young). We also compared the diet of pairs nesting in the mountains versus those nesting in the plains.

The location of territorial pairs and nest structures was plotted on topographic maps (Scale 1:50,000 and 1:100,000). Unused nest were attributed to the nearest pair holding a territory. We measured the diameter and external depth of the more accessible nests. Non-measured nests were classified in three morphological categories: (1) nests with external depth greater than diameter; (2) nests with the same external depth and diameter; (3) nests with external depth less than diameter. Assuming that the diameter is similar in all the nests (see results), the ratio external depth/diameter provides information concerning the quantity of accumulated nest material.

For estimating number of nests per territory and percent of breeding pairs we used only those territories that we were confident that we had found all the alternative nests. Breeding success was evaluated with the following indices: percent of breeding pairs = number of pairs that laid eggs/number of pairs monitored during the incubation period; mean number of young per pair = number of fledglings/number of pairs monitored; mean brood size at fledging = number of fledglings/number of pairs with fledglings.

RESULTS

Between September 1991 and February 1993 we found 49 territories occupied by pairs of adult Grey Eagle-Buzzards. Fourty-four territories were within the surveyed area, giving an estimated density of 1 pair/19 km^2. Density was higher on the plains (1 pair/13.2 km^2, N = 17) than in the mountains (1 pair/22.7 km^2, N = 27). Mean nearest-neighbor distance was 2081 m in the plains (SD = 916, range = 900–3900, N = 11) and 2964 m in the mountains (SD = 1445, range = 1500–6500 m, N = 14). The 1993 autumn survey indicated that adult birds generally remain in the territory throughout the year. We located four communal roosts of immature Grey Eagle-Buzzards, two of them within the study area. All were located on cliffs at heights ranging from 2 to 100 m above the ground, but occasionally some eagles roosted on the ground. The maximum numbers of immature eagles seen at any one time in each roost were 14, 8, 6, and 2. The two roosts inside the study area were used in both breeding seasons, but no eagles were observed at these roosts in the autumn of 1993.

We observed the eagles' daily routine in two roosts. Young eagles usually left the roost individually in the morning within one hour after sunrise. On two occasions we observed eagles leaving the larger roost in groups (8 and 14 individuals, respectively). The eagles returned individually to their roosts in the late afternoon, starting 4–5 h before dusk. On several occasions we observed the juveniles circling in groups over the roosting area late in the afternoon. During the study, four adult and six immature Grey Eagle-Buzzards were found dead. The cause of death was

TABLE 1

FOOD HABITS OF GREY EAGLE-BUZZARD BREEDING PAIRS AS DETERMINED FROM PELLETS FROM TWENTY DIFFERENT TERRITORIES IN THE ARGENTINEAN PATAGONIA

	Frequency of appearance	Percentage of pairs[a]	Minimum frequency[b]	Maximum frequency[b]
Mammals	80.79	100	61.90	92.80
Chaetophractus villosus	0.08	5	0	0.35
Zaedyus pichiy	0.16	5	0	6.90
Lepus europaeus	58.29	100	33.30	75.90
Rodents	19.16	85	3.10	33.40
Akodon sp.	0.08	5	0	0.35
Phyllotis darwini	0.33	15	0	2.70
Eligmodontia typus	0.08	5	0	1.30
Reithrodon auritus	0.72	25	0	4.50
Ctenomys sp.	2.80	40	0	13.00
Unid. rodent	15.16	80	0	23.20
Galictis cuja	0.40	15	0	1.80
Conepatus chinga	0.25	10	0	2.80
Cervus elaphus	0.08	5	0	2.30
Ovis aries	0.79	30	0	5.50
Unid. mammal	1.60	50	0	6.90
Birds	16.42	100	4.50	28.70
Theristicus caudatus	0.48	10	0	6.80
Anatidae spp.	2.64	40	0	10.75
Milvago chimango	0.08	5	0	0.40
Lophortyx californica	0.16	10	0	2.70
Fulica sp.	0.47	20	0	5.50
Rallidae spp.	0.24	5	0	1.55
Vanellus chilensis	0.48	20	0	3.10
Zenaida auriculata	0.08	5	0	0
Cyanoliseus patagonus	0.16	5	0	0
Colaptes pitius	0.08	5	0	3.40
Turdus falcklandii	0.08	5	0	1.30
Phyrgilus gayi	0.17	5	0	0.45
Sturnella loica	2.07	45	0	16.70
Passeriform spp.	0.88	30	0	8.10
Unid. bird (large size)	0.56	20	0	3.70
Unid. bird (medium size)	1.03	30	0	10.40
Unid. bird	6.69	70	0	16.60
Egg	0.08	5	0	0.40
Reptiles	1.74	40	0	9.50
Iguanidae	0.63	15	0	2.70
Ophidia	1.11	35	0	7.10
Fish	0.08	5	0	0
Salmonidae	0.08	5	0	0

TABLE 1
CONTINUED

	Frequency of appearance	Percentage of pairs[a]	Minimum frequency[b]	Maximum frequency[b]
Invertebrates	0.96	35	0	3.85
Crustacea	0.08	5	0	0.70
Orthoptera	0.16	5	0	2.50
Coleoptera	0.72	25	0	3.85
No. prey	1253			

[a] Percentage of pairs in which a certain prey category was recorded in the diet (N = 20).
[b] Minimum and maximum frequency of appearance recorded considering only the 14 pairs with more than 25 identified prey items.

established in five cases: four were shot and one was caught in a fox leghold trap.

We analyzed 1097 pellets from 26 localities throughout the study area and identified 1253 prey items (Table 1). The European hare (*Lepus europaeus*) accounted for 730 prey items (58.3%), followed by rodents (240 items, 19.2%) and birds (207 items, 16.4%). We also recorded as prey two species of carnivores (the hog-nosed skunk [*Conepatus chinga*] and the grison) [*Galictis cuja*], and occasionally reptiles (snakes and lizards of the family Iguanidae, 1.7%), and invertebrates (1.0%).

To test variation in the diet between the incubation and early nestling period versus the late nestling and postfleging period we analysed data from three pairs for which we had 25 or more prey items in each of the two periods. We considered four prey categories: European hare, rodents, birds, and other prey. Two of the three pairs showed significant differences ($\chi^2 = 23.724$, df = 3, $P < 0.001$, and $\chi^2 = 13.011$, df = 3, $P = 0.005$): the frequency of European hare in the diet increased during the second part of the breeding season, while the incidence of rodents and birds decreased (Table 2). In the third breeding pair there was a similar although not significant shift in diet ($\chi^2 = 5.214$, df = 3, $P = 0.1568$).

To study the differences in the diet between pairs in the mountains versus those in the plains we used only the data from the incubation and early nestling period of 11 breeding pairs (8 from the mountains and 3 from the plains) with 25 or more prey items. There were significant differences in the frequency of occurence of the four prey categories considered (European Hare, rodents, birds and other prey) in the diet of eagles in the mountains versus those in the plains ($\chi^2 = 17.385$, df = 3, $P = 0.0006$) (Table 3). Birds appeared more frequently as prey in the plain compared to rodents that were more frequent in the mountains (Table 3,

TABLE 2

FREQUENCY OF APPEARANCE OF PREY IN GREY EAGLE-BUZZARD PELLETS IN THREE TERRITORIES IN THE MOUNTAINS

	First period[a]			Second period[a]		
	A	B	C	A	B	C
European hare	50.4	45.5	46.6	73.8	76.5	59.2
Rodents	38.5	30.9	13.7	18.9	2.9	15.8
Birds	6.8	16.3	35.7	2.2	8.8	20.8
Other prey	4.3	7.3	4.0	5.1	11.8	4.2
No. prey	234	55	73	137	34	120

[a] Incubation and early nestling (first period) versus late nestling and post-fledging (second period).

$\chi^2 = 11.045$, df = 1, $P < 0.001$). Other prey were also significantly more frequent in the diet of pairs in the plain ($\chi^2 = 6.065$, df = 1, $P < 0.05$), but there were no significant differences in the frequency of European hare ($\chi^2 = 0.275$, df = 1, ns). There were still significant differences among the diets of individual pairs when considering only those nesting in the mountains (N = 8), and three prey categories (European hare, rodents and other prey; $\chi^2 = 86.012$, df = 14, $P < 0.0001$).

We located 101 Grey Eagle-Buzzard nests belonging to 28 different breeding pairs. The number of nests per pair ranged from 1 to 10 ($\bar{x}$ = 4.0, SD = 2.2). Eagles on the plains had a significantly higher number of nests (5.1 ± 2.2, N = 9) than those in the mountains (3.2 ± 2.0, N = 14, Wilcoxon-Mann-Whitney test, Z = 2.167, $P = 0.03$).

Nest dimensions were (N = 5): mean diameter 112.8 cm, SD = 7.0 cm, range = 104–122 cm; mean external depth 47.0 cm, SD = 17.9 cm, range = 20–70 cm. Nest morphology was estimated for an additional 91 nests, 68.1% had a diameter greater than the external depth, 24.2% had

TABLE 3

FREQUENCY OF APPEARANCE OF PREY IN GREY EAGLE-BUZZARD PELLETS IN TERRITORIES IN THE MOUNTAINS (N = 8) VERSUS THOSE IN THE PLAINS (N = 3)

	Mountains	Plains
European hare	51.9	54.3
Rodents	25.9	11.6
Birds	17.2	23.9
Other prey	5.1	10.1
No. prey	588	138

the same diameter and depth, and 7.7% had an external depth greater than the diameter. Nests with external depth the same or greater than diameter occurred significantly more on the plains 41.5% (N = 53) than in the mountains 18.4% (N = 38) ($\chi^2 = 4.422$, df = 1, $P = 0.035$).

Nest situation on the cliff (N = 85) was mainly on ledges (81.2%), vertical crevices (14.1%), and caves (4.7%). Only the 20.0% of the nests had some kind of rocky shelter. None of them were partially or totally concealed by vegetation.

We observed three clutches with two and one with three eggs (mean clutch size = 2.2). The proportion of eagle pairs that laid eggs was 80.9% (17 pairs seen incubating of 21 monitored during incubation). The percentage of pairs with at least one fledgling was 62.8% (N = 43). For the 43 pairs monitored, the mean productivity was 1.1 fledglings/pair/year; 16 pairs did not produce young, seven pairs had one fledgling, 19 pairs two fledglings, and one pair had three fledglings. Consequently, the fledging rate was 1.8 fledglings/successful pair (N = 27).

The number of fledglings per pair was similar in the two years both in the mountains (1991–92: 1.0, N = 6; 1992–93: 0.92, N = 16) and on the plains (1991–92: 1.72, N = 11; 1992–93: 1.33, N = 10) (Wilcoxon-Mann-Whitney test, $P > 0.05$). Pooling the data from the two breeding seasons, we found no significant difference (Wilcoxon-Mann-Whitney test $P > 0.05$) between the breeding success of birds on the plains (1.59, N = 21) and those in the mountains (0.87, N = 22). Human disturbance of reproduction was observed in only one case at a nest located on top of a power pole: it was removed with its contents (probably young nestlings) during maintenance tasks.

DISCUSSION

This study provides the first quantitative data on Grey Eagle-Buzzard population densities. Our density figures are in the higher ranges of those reported for large eagle species in the most favorable habitats (see Newton 1979). Jaksic and Jiménez (1986) suggest that the recent Grey Eagle-Buzzard population increase in southern Chile might be due to an increase in available prey (European rabbit and hare) and deforestation. In our study area, there has been no recent deforestation, but there has been a marked increase in the number of hares, which may well account for the high Grey Eagle-Buzzard density. In Europe the highest densities of large birds of prey are found in Mediterranean areas, where lagomorph densities are high (Soriguer 1981, Blondel and Badan 1976, Donázar 1988).

According to Jiménez and Jaksic (1990) the Grey Eagle-Buzzard has diminished in number in northern and southern Argentina because of secondary poisoning directed at controlling Culpeo Fox (*Dusicyon cul-*

paeus) and Crested Caracara (*Polyborus plancus*) populations. On the contrary, data from our study site and observations made while traveling to other places in Patagonia indicate that Grey Eagle-Buzzards are still abundant in Argentina (unpubl. data). In addition to the presence of exotic lagomorphs, there has been a drop in the use of strychnine in favor of more selective techniques of predator control (von Thungen 1991). We found few cases of direct attack on eagles by ranchers or their employees. The eagle conservation status may continue to improve because people are becoming more willing to believe that raptors play an important role in controlling diseases and rabbit populations. The European rabbit entered continental Argentina from Chile crossing the Andean range (Howard and Amaya 1975) and it is currently spreading close to the study area. In adjacent areas some claim that the rabbit causes severe damage to natural pastures, reducing food available to livestock (Amaya and del Valle 1983, Bonino and Amaya 1985).

Although many species of scavenging raptors use communal roosts at certain stages of their life (Newton 1979, Ceballos and Donázar 1990, Hiraldo et al. 1993), large eagle species generally do not (despite the scavenging habits of juveniles of these species, see Newton 1979). However, juveniles Grey Eagle-Buzzards proved an exception to this general rule: they formed communal roosts in our study area in spring-summer and were frequent visitors at hare and sheep carcasses (unpubl. data). Communal roosts are unusual among the members of the Buteoninae, the habit having been reported to our knowledge only for the Rough-legged Buzzard (*Buteo lagopus*) in winter (Freeman 1952).

In the study area, the Grey Eagle-Buzzard did not show a tendency to prey heavily upon birds and rodents, contrary to the findings of Jiménez and Jaksic (1990) in Chile. European hare was the most frequent prey item. Birds were preyed upon considerably less and at about the same rate as rodents. Data on the relative abundance of different prey in places were the diet of the Grey Eagle-Buzzard has been studied are not available precluding the possibility of finding a link between availability of prey and dietary preference. The proportion of hares in the diet of the Grey Eagle-Buzzard in our study (58.2%) is among the highest known for large eagles in temperate regions: in Golden Eagle diet, for example, the percentage of hares was 59.1% in Alaska (Ritchie and Curatolo 1982); 46.7% in Italy (Noveletto and Petretti 1980), 37.2% in Montana (McGahan 1968), 39.3% in the Alps (Mathieu and Choisy 1982), and 21.8% in the Pyrenees (Fernández and Purroy 1990). The increase in the proportion of hare in the diet towards the end of the breeding season might be due to an increase in hare density with the season, as it happens in other birds of prey whose diets rely heavily on lagomorphs (Fernández 1987, Don-

ázar 1989). Diet variations among pairs probably reflects differences in habitat composition. In our study area European hare and birds are not homogeneously distributed on the territory, they are much more abundant in "mallin" areas in the bottom of valleys than in arid zones of slopes and high plains (Novaro et al. 1992, unpubl. data).

Most Grey Eagle-Buzzard nests in our study area were on cliffs (92.0%, N = 101; Travaini et al. 1994). It is striking how noticeable these nests can be. Eighty percent of them were located in very exposed sites. No nest was found concealed by vegetation or hidden inside cavities in the rock, contrary to what is commonly observed in other large eagles of temperate regions (Fernández and Leoz 1986). In addition, the Grey Eagle-Buzzard seems to have a relatively high number of nests per breeding pair (mean = 4.0, range = 1–10). The average tends to be in the upper limit of those observed in other populations of big eagles. For example, Golden Eagles in Spain have 2.1–3.3 (Jordano 1981, Fernández and Leoz 1986); in the Alps and the Apennines, 2.4–4.0 (Fasce 1979, Mathieu and Choisy 1982); in Britain 3.1–5.1 (Watson 1957, Brown 1969), and 6.0 in Idaho (Beecham and Kochert 1975). In our opinion, the lack of human harassment of the Grey Eagle-Buzzard population could account for the high number of nests located in exposed locations. In contrast, in Europe, where human persecution has been intense, large eagles may have been forced to nest in more concealed locations (Fernández 1993, Fernández and Leoz 1986). Grey Eagle-Buzzards, like other raptors, may use eyries as territorial markers (Newton 1979). In support to this idea, in the plains, were the eagle density was greater, both the number of nests per breeding pair and the relative size (the relation between external depth and diameter) of the nests was greater than in the mountain zone.

The proportion of pairs that tried to reproduce (80.9%) and those that successfully raised at least one young (62.8%) fall within the range reported for other large eagles (see Newton 1979). Regarding brood size, the only previous data available from five nests in Chile reported one chick per nest in all cases (Jiménez and Jaksic 1990). The Grey Eagle-Buzzards in our study reared one to three chicks, two being the most common number. This suggests that if the species is capable of siblicide behavior, the behavior may be strongly influenced by food availability as occurs in other large eagles and raptors (Delibes et al. 1975, Newton 1979, Gargett 1990).

ACKNOWLEDGMENTS

Miguel Delibes, Alejandro Rodríguez, Obdulio Monsalvo, and Miguel Pineda helped with the field work. Our thanks to the administrators of the Estancias Cerro de los Pinos, Chimehuín, Collun-Có, Collón-Curá, Lolén, Pilolil, and Quemquemtreu, who permitted us to

work in their estates. Logistic support was provided by the Centro de Ecología Aplicada del Neuquén (Argentina); we are very thankful to Alejandro del Valle and Antonio Guiñazú for their continuous help, and to Dra. Marta Piantanida and Dr. Jorge R. Navas from the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" for their help with reference collection. Sonia C. Zapata identified mammal species from hair medulla type and scale patterns. Financial support was provided by the Instituto de Cooperación Iberoamericana and the Ministerio de Asuntos Exteriores (Spain) through the Programa de Cooperación Científica con Iberoamérica. Ignacia de Bustamante and William Safranek helped with the English translation.

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Wilson Bull., 107(4), 1995, pp. 686–697

HABITAT USE AT NIGHT BY WINTERING AMERICAN WOODCOCK IN COASTAL GEORGIA AND VIRGINIA

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Abstract.—Nocturnal habitats used by American woodcock (*Scolopax minor*) were studied using radio telemetry at two coastal wintering sites in Georgia (1982–84) and Virginia (1991–92). In Georgia, use of forested habitats at night was extensive while use of fields at night varied between years but generally was low. We found no difference in the probability of moving to a field at night among the four age-sex classes ($P = 0.23$). A significant effect ($P < 0.05$) of age-sex class was noted between distances moved from diurnal to nocturnal locations in Georgia. Young females moved farther than any other age-sex class. In Virginia, no effect of age-sex class was found on the probability of being located during the night in either a field or a forest. Received 30 June 1994, accepted *15 May 1995.*

Wintering American woodcock (*Scolopax minor*) frequent both forests and fields at night (Roberts 1993). During the night on the wintering grounds, woodcock conduct two main activities, feeding and roosting (Roberts 1993). At night on the winter grounds, unlike on the summer grounds, woodcock feed so extensively (Glasgow 1958, Dyer 1976, Stribling and Doerr 1985) that most food requirements probably are met at this time (Dyer 1976, Roberts 1993). In addition to feeding, roosting occurs at night (Glasgow 1958, Dyer 1976, Britt 1971, Connors and Doerr 1982). Roosting in fields may reduce predation (Connors and Doerr 1982). As evidence of their vulnerability to predation at night, woodcock have developed supposed anti-predator behaviors while roosting, e.g., non-random positioning in roosting fields (Connors and Doerr 1982). The need for such behaviors can be understood since survival rates on the wintering grounds generally are low compared to other times of the year (Krementz et al. 1994). In an average winter along the Atlantic coast, about 20% of arriving woodcock are depredated before spring migration (Krementz et al. 1994). While some work has been done on roosting behavior and characterizing openings used at night by wintering woodcock (Roberts 1993), only a single study has followed individual woodcock to determine the frequency of use and variety of habitats used at night. Horton and Causey (1979) monitored radio-marked woodcock in the Piedmont of Alabama and found that slightly more observations occurred in forested areas (56%) than in openings (44%), and that a variety

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of habitat types (≥5) were used. An age-sex class effect on use of openings versus forests at night was found with adult males and immature females using openings and forests equally, young males using openings more than forests, and adult females using forests more than openings (Horton and Causey 1979).

Because woodcock populations in eastern North America have declined since the 1970s (Kendall and Bruggink 1994), and because our understanding of the variety of habitats used at night as well as the frequency of use of those habitats is not well known (Horton and Causey 1979, Roberts 1993), we initiated a study, in part, to document the variety of habitats used at night and to investigate the effects of age and sex on habitat use at night. We also report here previously collected data designed to address these same concerns (G. Haas and J.T.S., U.S. Fish Wildl. Serv., unpubl. data).

STUDY AREAS AND METHODS

We used two study sites: coastal Georgia and Virginia. The first study area was along the southern shore of the Altamaha River near Everett, Georgia. The predominant land use was timber managed primarily for pine pulpwood. Pine plantations were clear-cut followed by intensive post-cutting management including windrowing, seed-bed preparation, fertilization, planting with loblolly pine (*Pinus taeda*) or slash pine (*P. elliottii*), and sometimes herbiciding. Society of American Foresters (SAF) (Anonymous 1975) forest cover types represented at this site included loblolly pine, loblolly pine-hardwood, sweetgum-nuttall oak-willow oak (*Liquidambar styraciflua, Quercus nuttallii, Q. phellos*), overcup oak-water hickory (*Q. lyrata, Carya aquatica*), baldcypress-water tupelo, (*Taxodium distichum, Nyssa aquatica*), water tupelo, sweetbay-swamp tupelo-red maple (*Magnolia virginiana, N. sylvatica, Acer rubrum*). We lumped all forest types which contained a predominance of oaks in wetter sites into the SAF type group, bottomland hardwood. Four small (<5 ha) corn fields and six pastures (5–50 ha) were located within 3 km of the center of the study site. The corn fields were disked in the fall leaving little crop residue. The pastures ranged from lightly to heavily grazed. The second study area was the Eastern Shore of Virginia National Wildlife Refuge (ESVNWR) and adjacent farmlands located on the southern tip of the Delmarva Peninsula near Cape Charles, Virginia. It was characterized by agricultural fields scattered among older woodlots of mixed pine-hardwood. Little forest management was evident in the area. SAF forest types included black cherry (*Prunus serotina*), black locust (*Robinia pseudoacacia*), loblolly pine, loblolly pine-hardwood, and sweetgum-yellow poplar (*Liriodendron tulipifera*). We also included 1 non-forest habitat type, waxmyrtle (*Myrica* spp.). Agricultural crops ≤5 km from the refuge included soybeans, corn and winter wheat. All crops were usually disked in the fall, making them relatively flat with virtually no crop residue. No fallow croplands were available ≤2 km from the refuge. Two fallow soybean fields between two and three years old, and a single abandoned grass airstrip were located on the refuge. None of the six fields on the refuge nor any fields nearby (≤5 km) were either clearcuts, regrowth, or pine <3 m (see below).

We classified all managed pine sites by age. Managed pine plantations were classified as (1) pine <3 m—sites planted with pines and usually <5 growing seasons, (2) pine 3–9 m—sites planted with pines and usually 5–15 growing seasons, and (3) pine >9 m—sites planted with pines and usually >15 growing seasons. We classified all pine sites which were not

managed after cutting as (1) clearcut—<1 growing season old, (2) regrowth—between one and three growing seasons old, and (3) shrubland—>3 growing seasons old. The latter two types were predominantly occupied by blackberry (*Rubus* spp.), oak (*Quercus* spp.) saplings, and broom sedge (*Andropogon virginicus*). We further classified habitat types into forested and field types. Fields included clearcuts, regrowth, shrubland, pine <3 m, cropland, and pastureland. Under the definition that a field is an area without a tree canopy that is closed, then the inclusion of pine <3 m tall as a field type is clear cut. As an indication that pine <3 m should be a field type was the observation that male woodcock regularly performed aerial courtship flights at these sites (D.G.K., unpubl. data). All other habitat types were considered forested.

Both study areas were characterized by relatively mild winter weather. The mean number of days with the daily minimum temperature ≤0°C during December–February recorded at the weather stations closest to the study areas were: Norfolk, Virginia–45; and Waycross, Georgia–30 (1951–75 period, NOAA 1978). Soil temperatures at 10 cm depth were rarely <0 C (NOAA 1982–92); any freezing of surface soil was of short duration.

Study sites were not monitored simultaneously. Study dates were: (1) Georgia: December 1982–February 1983, December 1983–March 1984, and (2) Virginia: December 1991–March 1992.

Woodcock were initially located at each study site by conducting crepuscular flight surveys at openings (Glasgow 1958) and by searching openings for the presence of probe holes and feces (Glasgow 1958, Boggus and Whiting 1982). Once sites with woodcock were located, we captured woodcock using ground traps (Liscinsky and Bailey 1955), mist nets (Sheldon 1971), and nightlighting (Riefenberger and Kletzly 1967). Upon capture, woodcock were banded with a U.S. Fish Wildlife Service leg band, weighed, aged and sexed (Mendall and Aldous 1943, Martin 1964). A radio transmitter was attached dorsally between the wings using either monofilament line or a single multi-strand wire loop harness and livestock tag cement (McAuley et al. 1993). Transmitters weighed 3.5–5.0 g (≤3% of body mass).

We radio-marked all woodcock captured each year before 31 January. Marked birds were tracked daily from vehicles with 4- or 6-element yagi antennas. Lost (censored) birds were searched for by air (Gilmer et al. 1981) within a 50 km radius of the capture sites.

In Georgia, birds were monitored four times daily, once every 6 h. Time permitting, each bird was approached on foot to <8 m. To ensure that the location was positive, the marked bird was circled (McAuley et al. 1993). Otherwise, locations of birds were estimated via triangulation. No investigation of telemetry location error was conducted. Locations were plotted to the nearest 50 × 50 m block on a USGS 7.5 min series map during each of the four monitorings. The date, time and cover type at the location of the bird were recorded. Sometimes woodcock moved into fields at night and then returned to forested sites during the same night. In these cases, we recorded that the bird did use a field at night. We estimated the distance moved between the location of the bird during the afternoon and its location that night to the nearest 50 m. Again, if the bird moved to a field and then returned to the forest, we recorded the distance that it moved to the field.

In Virginia we monitored the exact location of the marked birds diurnally by circling the bird on foot. Nocturnally, we monitored whether marked birds were in forested or field habitats, but nocturnal locations were not taken daily. We attempted to record nocturnal locations every other day. All fields used were bordered by roads allowing us to determine if a radio-marked woodcock was in a field or not. We only monitored birds after the evening crepuscular period until 23:00 h. Some woodcock could have moved into the fields after this time and been undetected.

Between the diurnal and nocturnal location, each woodcock had three possible responses: (1) no measurable movement, (2) a measurable movement but remained in the same habitat

type, and (3) a measurable movement and moved to a different habitat type. We decided to analyze the data taking into consideration our confidence in determining the location of a woodcock at night. At the most accurate level, our analyses assumed that we could locate each bird accurately and precisely. These analyses were based on categorizing movements into no movement between the diurnal and nocturnal location (nocturnal location − diurnal location = 0 m), and any movement between diurnal and nocturnal location (nocturnal location − diurnal location > 0 m). The next level of analyses assumed that we could determine the cover type accurately. These analyses used no change in habitat type between the diurnal location and nocturnal location as no movement versus a change in habitat type between the diurnal and nocturnal location as a movement. Thus 2 levels of accuracy were pursued in these analyses.

To investigate potential effects of age and sex on movement, we modeled the number of movements between habitats (forest to field) for each bird as a binomial random variable with the movement rate parameters within each age-sex class following a beta distribution. This allowed for each bird to have its own movement rate and sample size. We used likelihood ratio tests to compare the means of the beta distributions among the age-sex classes. This tested whether average movement rates varied among the age-sex classes. We used the same procedure with data from young males, which had reasonable sample sizes in both years, to test for differences in movement rates between years.

The next analysis used a four-factor ANOVA to examine whether the average distance moved between diurnal and nocturnal locations differed between ages, between sexes, and whether or not habitat changed. Factors were ages, sexes, movement, and individual woodcock (nested within age and sex classes). Sums-of-squares appropriate for unbalanced designs (SAS 1990; type III model) were used; the mean-square for the individual was used as the error term to test for age and sex effects and Satterthwaite's adjustment was used to estimate the appropriate degrees-of-freedom (Milliken and Johnson 1984). Observations were restricted to dates where more than five individuals were monitored daily.

In Virginia, the irregular nocturnal monitoring precluded us from examining the effects of age and sex on movement probability or distance moved. However, we felt that we could investigate whether age or sex affected the probability of moving into a field or remaining in forested habitat nocturnally. We did so using a two-way ANOVA. Only woodcock monitored more than five times were used in these analyses.

RESULTS

Of the 21 woodcock captured in 1982–83, only three were adults which precluded analyzing age effects and only four were females precluding analyzing sex effects (Table 1). Sample sizes in 1983–84 were much better for adults (Table 1), and we were able to examine age-sex class effects in that year. Sixteen woodcock were removed from analyses in 1983–84 because they were observed less than five times each. Adult males were also poorly represented in the Virginia sample, and adults were less common than young (Table 1). We chose to examine age effects in Virginia. Only two young woodcock from Virginia were excluded from analyses because they were observed <5 times each.

Georgia

In Georgia no radio-marked woodcock used cropland or pastures at night in either year. In 1982–83, we spotlighted both habitat types 10

TABLE 1

SAMPLE SIZES BY AGE, SEX, LOCATION AND YEAR OF AMERICAN WOODCOCK WINTERING IN COASTAL GEORGIA AND VIRGINIA[a]

	Young males	Young females	Adult males	Adult females	Total
Georgia 1982–1983	10 (3)	3 (2)	2 (0)	1 (0)	16
Georgia 1983–1984	22 (4)	11 (6)	10 (4)	7 (2)	50
Virginia 1991–1992	27 (1)	34 (1)	2	7	70

[a] Numbers in parentheses represent the number of birds captured, observed <6 times, and not used in analyses.

times in December and January (70 h total) and observed no woodcock. Based on experiences in 1982–83, we did not spotlight either habitat type in 1983–84.

Virtually all woodcock during both years made measurable movements between their diurnal and nocturnal locations (367 of 386 observations in 1982–83, 899 of 938 observations in 1983–84). In 1983–84, no age-sex class effects were found when we compared those age-sex classes moving versus not moving for: (1) woodcock making a movement to any habitat type ($\chi^2_3 = 2.33$, $P = 0.51$), (2) woodcock making any movement and ending up in forested habitats ($\chi^2_3 = 4.55$, $P = 0.21$), and (3) woodcock making any movement and ending up in field habitats ($\chi^2_1 = 1.80$, $P = 0.18$). No age-sex class effects were found for any of these tests because virtually all woodcock moved during the crepuscular period.

During both years, woodcock were usually located in forested habitat types during the day (Table 2). In particular, bottomland hardwoods were used extensively during the day (82%, 1982–83; 78%, 1983–84). In 1982–83, woodcock moved from bottomland hardwoods most often to pine plantations with pines <3 m tall (62%, Table 2), followed by remaining in bottomland hardwoods (32%). We did not test the effects of age-sex class on use of habitat at night in 1982–83 because of small samples, but in total, woodcock either remained in or moved to fields about 67% of the time. Most of the movement to fields was to the pine <3 m type (93%, Table 2).

In 1983–84, woodcock remained at their diurnal location 35% of the time, while they moved to a different location at night that was forested 52% of the time, and they moved to a different location at night that was an opening during the remaining 13% of the time (Table 2). When woodcock were located in forested habitat during the day, they typically remained there at night (743 of 861 observations).

TABLE 2

NUMBERS OF OBSERVATIONS OF RADIO-MARKED AMERICAN WOODCOCK WINTERING IN COASTAL GEORGIA DURING 1982–1983 AND 1983–1984

	To nocturnal location						
	Pine <3 m	Pine 3–9 m	Pine >9 m	Bottom-land hardwood	Cypress-tupelo	Clearcut/ Re-growth/ shrub-land	Σ
From diurnal location				1982–1983			
Pine <3 m	23	1	0	2	0	1	27
Pine >9 m	0	0	1	0	0	0	1
Bottomland hardwood	197	2	0	101	2	14	316
Cypress-tupelo	3	0	0	0	0	0	3
Clearcut/regrowth/shrubland	6	10	0	3	0	20	39
Σ	229	13	1	106	2	35	386
Only from bottomland hardwood							
Young male (10)[a]	125	0	0	52	0	13	190
Young female (3)	40	0	0	29	2	1	72
Adult male (2)	26	0	0	3	0	0	29
Adult female (1)	6	2	0	17	0	0	25
Σ	197	2	0	101	2	14	316
From diurnal location				1983–1984			
Pine <3 m	0	1	0	0	0	0	1
Pine 3–9 m	8	51	0	13	2	4	78
Pine-hardwood	0	1	0	0	1	0	2
Bottomland hardwood	60	418	0	215	9	40	742
Cypress-tupelo	1	16	0	7	10	5	39
Clearcut/regrowth/shrubland	9	20	0	9	4	48	90
Σ	78	507	0	244	26	97	952
Only from bottomland hardwood							
Young male (22)	24	201	0	82	7	17	331
Young female (11)	10	83	0	38	0	10	141
Adult male (10)	19	72	0	56	1	7	155
Adult female (7)	7	62	0	39	1	6	115
Σ	60	418	0	215	9	40	742

[a] Numbers in parentheses are number of woodcock.

We found no relationship between age-sex class and the probability of a woodcock moving to either a forested or a field habitat at night (χ^2_3 = 4.29, P = 0.23).

For young males, no difference (χ^2 = 1.28, df = 1, P = 0.26) was found between years in the probability of moving from a diurnal location to another location.

Distance Moved

The distance moved between diurnal and nocturnal locations did not differ by age ($F_{1,50.9} = 0.13$, $P = 0.72$), sex ($F_{1,49.3} = 1.16$, $P = 0.29$), or age-sex ($F_{1,49.6} = 0.60$, $P = 0.44$). Distance moved did differ by whether or not a bird changed habitats ($F_{1,73.3} = 55.20$, $P < 0.001$) with woodcock that changed habitats moving farther ($\bar{x} = 708$ m) than those that did not ($\bar{x} = 310$ m). Breaking down these data by whether a woodcock moved from its diurnal location to either a forested habitat or to a field habitat affected this latter outcome. Distances moved by woodcock moving to forested habitats did not differ according to age-sex class ($F_{1,30.75} = 1.59$, $P = 0.22$). An age-sex effect on the distance moved between diurnal covers and fields at night was evident ($F_{1,4.85} = 4.69$, $P = 0.08$). Further examination of this pattern revealed that there was an effect of age on distance moved to fields at night ($F_{1,4.94} = 8.97$, $P = 0.03$). Adults moved shorter distances to fields than did young woodcock.

Between years, young males showed no difference ($F_{1,726} = 0.02$, $P = 0.90$) in distances moved.

Virginia

Six fields on the refuge were used nocturnally whereas no fields off-refuge were used by radio-marked woodcock despite woodcock using forested habitats off-refuge during the day. During five evening crepuscular surveys at three off-refuge fields, no woodcock were observed. Marked birds frequenting off-refuge habitat diurnally would return to refuge fields nocturnally from up to 1.1 km away. Of the 24 marked woodcock moving off-refuge, 19 returned at least once to use nocturnal fields. Woodcock moving off-refuge did not move far ($\bar{x} = 1.9$ km, SE = 0.870).

No effect of age ($F_{1,64} = 0.09$, $P = 0.77$), sex ($F_{1,64} = 0.09$, $P = 0.77$), or age-sex ($F_{1,64} = 0.12$, $P = 0.74$) was found on the probability of being observed in woods (213 observations) versus fields (271 observations) on the refuge at night. The effect of age on nocturnal location is tenuous, though, as the sample size for adults was small (Table 1).

DISCUSSION

Horton and Causey (1979) found that, on any given night, 43% of marked woodcock in the Piedmont of Alabama were located in open fields. They also found significant differences by age-sex class in use of fields versus woods at night. They found that young males used fields more often than forests, young females and adult males neither preferred nor avoided fields, and adult females used forests more often than fields (Horton and Causey 1979). The use of forests by adult females was ques-

tioned, though, as half of the observations were located within 27 m of a field edge, thus half of the adult females were located 'on' a field edge. Horton and Causey (1979) noted that 27 m was the mean error in exactly locating a bird. We point out that the chi-square analysis Horton and Causey (1979) used incorporated individual observations as replicates rather than the more appropriate factor, individual birds. In not doing so, within individual variation is bound up with among individual variation and the number of replicates is misleading (B. Cade, Natl. Biol. Serv. pers. comm.). For example, not taking into account this problem, our original test results (unpubl. data) indicated the exact same age-sex patterns in moving to fields versus forests at night as was found by Horton and Causey (1979). After changing our analyses, we found no relationship between age-sex class and moving to fields versus forests at night.

Our data suggested that fields were used at night but they were not used often in Georgia. The use of fields nocturnally was year-dependent with much greater use in 1982–83 than in 1983–84. The large discrepancy in field use by year (65%, 1982–83; 13%, 1983–84) may result from our definition of field habitat. In 1982–83, 62% of all observations were in pine plantations <3 m high. Some researchers may argue that this category may not constitute 'field' habitat because the canopy was beginning to close. Excluding these observations in 1982–83 only 3%, and in 1983–84 only 5% of all birds moving ended up in clearly field habitat, clearcut, shrubland or regrowth. Excluding the pine <3 m habitat type from the field category would result in field use at night being an uncommon event, <10% of the time. Field use in Virginia was much higher, about 50% of all observations. But use of fields was specific to those fields found at the refuge. Those fields, fallow soy beans and an abandoned grass airstrip, were attractive enough to radio-marked woodcock to cause them to move up to 1.1 km during the crepuscular period. The croplands at Virginia and Georgia and the pastures in Georgia were not attractive to roosting woodcock. The lack of use of croplands at Virginia must have resulted from the management practice of removing all residual crop materials and tilling the soil flat. Similar findings have been reported by Glasgow (1958) and Connors and Doerr (1982). Residual crop materials were left on the croplands in Georgia yet still no use at night by woodcock was observed. We can only speculate that the small size of fields encountered (<5 ha) contributed to the lack of use of those fields. Size was not a factor with the lack of use of pasturelands in Georgia though as fields varied from 5–50 ha. Glasgow (1958) found that heavily grazed fields were little used by woodcock at night, but both moderately and lightly grazed pastures were available in Georgia. We cannot explain the lack of use of pastures in Georgia. Based on our findings, we hypothesize that given a choice

between field types (cropland, pastureland, clearcut), woodcock will choose clearcuts over other field types.

Although our findings suggest that the use of fields is not common, we strongly believe that the availability of fields to roost, perform courtship activities and feed in is important. In searching for woodcock to capture at the beginning of each field season, we noted that most fields had no birds, a few fields had some birds (3–10), and one or two fields had tremendous numbers of woodcock (>50). Clearly these latter fields were preferred over others, and importantly, the location of these fields must have affected where woodcock were locating themselves diurnally as woodcock moved no more than 1.1 km to a nocturnal field. We hypothesize that these fields were attractive because of their size, location relative to preferred diurnal habitat, amount and height of ground cover.

The shift in use of managed pine sites at night between years at Georgia reflects the availability of the two habitat types between years. Between 1982–83 and 1983–84, most of the pine <3 m grew into the next type, pine 3–9 m. Thus, the increased use of pine 3–9 m in 1983–84 indicated that woodcock were using what was available rather than a shift in preferences between years. Use of managed pine sites during the day was found to be in accordance to the amount of habitat available (Krementz and Pendleton 1995).

If our data are representative of the norm, then the use of relative abundance data collected on fields at night during the winter would clearly underestimate the true number of birds in the general area being surveyed (Tappe et al. 1989). This would not be a problem in deriving inferences about population trends on wintering grounds unless the proportion of woodcock frequenting fields at night is year-dependent. Our data from young males did not suggest a year effect on probability of movement. If there are year effects on field use at night, then numbers of woodcock counted using fields would be confounded with time and no valid inferences regarding population trends could be legitimately drawn.

Horton and Causey (1979) monitored distances moved during the crepuscular period and found most birds moved >100 m (65% of observations) with a mean of 183 ± 28 m. Our findings for those birds moving from one habitat type to another habitat type differed greatly with crepuscular flights being, on average about 700 m. In Georgia, the bottomland hardwoods frequented diurnally were quite extensive, >1 km wide. Woodcock would typically move quite far into these bottomland stands during the morning crepuscular flight. Examination of the study area map of Horton and Causey (1979) suggests that deep bottomland hardwoods were not available. Without the option of extensive bottomland hard-

woods, woodcock apparently had no choice but to remain close to openings and so fly shorter distances during the crepuscular period.

Most data on age ratios of woodcock captured in nocturnal fields indicate that adults are captured less often than young (Dwyer et al. 1988, Roberts 1993, Sepik and Derleth 1993). Several hypotheses have been offered to explain this phenomenon including: (1) adults frequent nocturnal fields less often than do young (Gregg 1984, Owen and Morgan 1975, Sepik and Derleth 1993), (2) fewer adults are available to capture than young (Sepik and Derleth 1993), and (3) adults are less easily captured than young (Connors and Doerr 1982).

Our data do not support the first hypothesis as adults were as likely to frequent fields nocturnally. Rather, our data suggest that adults are less abundant, or they are less easily captured. Based on band recovery data, Martin et al. (1965) found that young woodcock were more likely to be shot nearer the Atlantic coast than inland compared to the probability of shooting an adult. They hypothesized that this pattern was a consequence of young woodcock being diverted eastward because of prevailing westerly winds. Thus, our coastal study sites should have a preponderance of young woodcock. Connors and Doerr (1982) observed that adult woodcock were nonrandomly distributed in nocturnal fields with adults tending to frequent the edges of fields rather than the interior sections. This observation was also made by Horton and Causey (1979). The close proximity to the field edge may enable adult woodcock to walk or fly to escape cover quickly, and so avoid capture.

ACKNOWLEDGMENTS

We acknowledge W. L. Link for statistical consultation, G. H. Haas for access to unpublished data, and G. W. Wood, D. Carlson, S. Kyles, and S. W. Stairs for logistical support. Georgia-Pacific Corporation, International Paper Company, Union Camp Corporation, and Westvaco allowed access to their lands. We also thank D. A. Clugston, M. N. Nelson, R. T. Speer, D. Rheinhold, C. Parrish, M. V. Slivinski, J. B. Berdeen, and T. Helm for assistance in collecting data. We also thank B. S. Cade and two anonymous reviewers for comments on the manuscript. Support was provided by Patuxent Wildlife Research Center, Ruffed Grouse Society, Eastern Shore of Virginia National Wildlife Refuge, and Georgia Department of Natural Resources.

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ABUNDANCE AND DISTRIBUTION OF OVERWINTERING PASSERINES IN BOTTOMLAND HARDWOOD FORESTS IN NORTH CAROLINA

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ABSTRACT.—We investigated the abundance and distribution of passerines overwintering in natural levees, and tupelo (*Nyssa aquatica*) and cypress (*Taxodium distichum*) swamps along Roanoke River bottomland hardwood forests, North Carolina, in 1991–93. A total of 21 species, 10 resident and the remaining temperate migrants, was recorded during the study. The mean number of passerines was significantly higher ($P < 0.05$) in levee than in swamps. Resident species were significantly ($P < 0.05$) more abundant than temperate migrants within and between levees and swamps. Plant species richness and low vegetation components (e.g., horizontal cover, density of seedling/saplings) accounted for significant proportions of the variability in bird abundance within and across vegetation types. Canopy cover and density of overstory trees also predicted bird abundance, particularly for nuthatches in swamps. *Received 1 Nov. 1994, accepted 20 May 1995.*

Habitat loss and declines in abundance of some resident bird species and temperate migrants have focused attention on the need for knowledge of their overwintering ecological requirements to address year round conservation needs (Hunter et al. 1993, in press). Unfortunately, such information is limited (e.g., Dickson 1974; Root 1975; Kennedy 1977; Yahner 1985; Morrison et al. 1985, 1986; Remsen et al. 1989).

Previous studies have reported diverse breeding and overwintering bird communities in forested wetlands (Dickson 1978, Blem and Blem 1975, Kennedy 1977, Hamel 1989). However, because data on avian winter ecology in this habitat are scant, the importance of forested wetlands to resident species and temperate migrant abundance, survival and breeding success may be underestimated. A similar possibility has been noted for wintering habitats of neotropical migrants (Petit et al. 1993). Here data are presented on species composition, abundance, and distribution of overwintering Passeriformes (passerines) in natural levee and tupelo-cypress swamp forests along the Roanoke River Floodplain, North Carolina. The Roanoke River Floodplain includes the largest intact, and least disturbed, bottomland forest remaining in the Mid-Atlantic Region (Stolzenburg 1993). Relationships between passerine abundance and vegetation structural diversity were examined, and discussed in light of present management practices.

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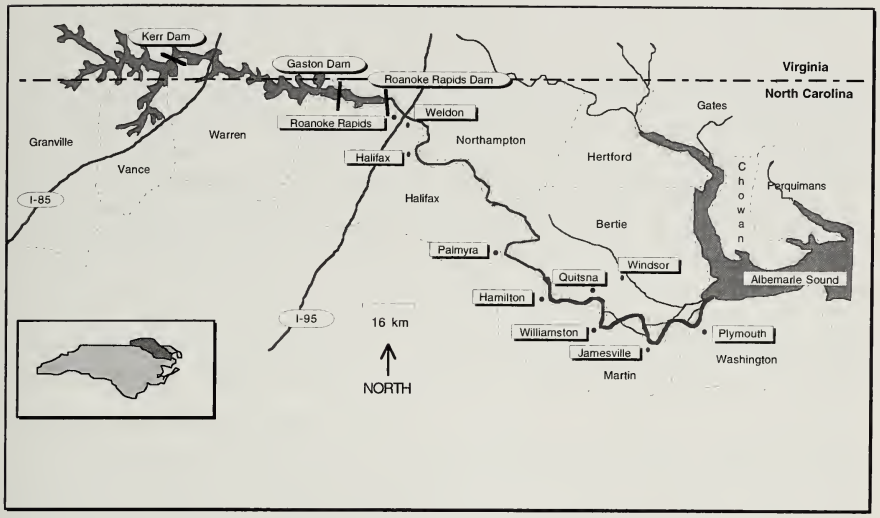

FIG. 1. Map of the lower Roanoke River Floodplain, North Carolina.

STUDY AREA AND METHODS

The Roanoke River Floodplain is approximately 354 km long and drains approximately 24,800 km^2 (Lea 1991) (Fig. 1). Three dams were built on the Roanoke River near the Virginia-North Carolina state line between 1950 and 1963 for hydroelectric power and flood control. Vegetation in the floodplain has been categorized into 20 different community types (Schafale and Weakley 1990). Tupelo-cypress dominated swamps and natural levees were selected for this study because they represent the most extensive vegetation types in the floodplain, and hence, an appropriate benchmark to develop baseline data. The tupelo-cypress swamps in this region are generally flooded for substantial parts of the year (e.g., 1–3 mo.) (Schafale and Weakley 1990). Natural levee communities occur adjacent to the river channel and are dominated by common bottomland hardwood species [e.g., box elder (*Acer negundo*), sweetgum (*Liquidambar styraciflua*), and green ash (*Fraxinus pennsylvanica*)]. Levees are seasonally to intermittently flooded during winter and spring.

Temperate migrants were defined as North American breeding species migrating within the North American continent, north of Mexico (Hunter et al. 1993), and include the Roanoke River as part of their wintering range. Permanent residents were those species present along the Roanoke year round. Their populations were censused using the fixed radius point count method (Hutto et al. 1986). Census data were collected along four (1991–92) and 16 (1992–93) transects, equally allocated between natural levee and tupelo-cypress study areas (i.e., forest tracks), and at least 150 m from any edges (e.g., river bank, plant community types). Each transect had four (1991–92) and three (1992–93) count stations placed at 150 m intervals. Data from one swamp transect (1992–93) were later discarded from analyses because the vegetation features on this transect were more characteristic of a levee-swamp ecotone. Study areas were established between Halifax and Jamesville, North Carolina, downstream from the dams (Fig. 1). Study areas in swamps ranged in size from 340 to 2500 ha; in natural levees, they ranged from 70 to 200 ha.

Biweekly counts, at each transect, were made when possible from mid-December through

the end of February, 1991–1992. In 1991–92, counts were scheduled twice weekly. However, actual total visits to each transect ranged from 12 to 15 due to unexpected flooding conditions. A total of seven visits were made in 1992–93, every two weeks on the average. At each station, birds were counted for 10 min and individuals identified to species by call or sight. All detections were recorded as either inside or outside a 30-m radius (Anderson and Ohmart 1981, Blondel et al. 1981). To minimize duplicate counts, we recorded approximate position and direction of detections on station diagrams divided into quadrants along cardinal axes. Individuals flushed from within the station radius, as we approached each count station, were recorded as inside detections (Hutto et al. 1986). To complete censusing all transects within 2–4 days, count stations were visited from 07:00 and 15:30 h in 1991–92 and 07:00 through 13:00 h in 1992–93. Analyses of 1991–92 data showed that there were no significant differences in the number of detections due to time of day for 75% of the passerines (Zeller 1994). To minimize bias for species with time of day dependence and also to minimize observer biases, starting times and observers were alternated among transects and vegetation types.

Vegetation at each station was sampled in 1992–93 following procedures described by Martin and Geupel (1993). Four subpoints were established at each count station. The first subpoint was centered at the count station (marked by a stake) and the three remaining ones were located at 120° from each other around the central subpoint. The direction of the first outer subpoint was randomly located (e.g., 0–359°). The center of the outer subpoints was located 25 m from the count station center. Canopy height was measured at each subpoint using a clinometer, and vegetation was categorized as (1) all shrubs and saplings (<10 cm dbh) within a 5 m radius circle, and (2) all trees (≥10 cm) within an 11.3 m radius circle. In addition, vegetation data were grouped by timber-size classes: 1) stem (<2 cm dbh); 2) seedling/sapling (2–12 cm); (3) pole (13–27 cm); (4) small saw (28–37 cm); and (5) large saw (≥38 cm). Vegetative cover (i.e., horizontal and canopy cover) was estimated using ocular tubes (James and Shugart 1970). Readings were made at all subpoints. Horizontal cover readings were taken in each of the four cardinal directions (N, S, E, W) within a 30 m radius from the subpoint centers at hip level (approx. 0.60 m). Positive horizontal readings were recorded as either woody or herbaceous vegetation. Canopy cover was recorded at four 5 m intervals between the center and each of the 3 outer subpoints.

Although census data were collected on all passerines, blackbirds (i.e., grackles, cowbirds, starlings) were deleted from the data set because their presence on the study areas was erratic, consisting of large flocks (1,000's of individuals). Crows were also deleted because many detections were outside the areas of interest. Census data were expressed as mean total detections per count station. Total detections for a given census occasion was the sum of counts inside 30 m, outside, and flushed. Standard errors were estimated using station means, not weekly counts per station, to avoid bias caused by repeated measures (Hurlbert 1984). Total detections were used for the analyses because they met assumptions of normality and homogeneity of variances (Shapiro-Wilk and Bartlett tests, JMP, SAS Inc. 1994). Count data within 30 m were non-normal, skewed towards zero. Avian abundance levels and vegetation structural parameters between vegetation community types were compared using *t*-tests. Tests comparing abundance between vegetation community types were conducted only if a bird species was noted in both habitat types. Backward stepwise regression analyses on non-transformed habitat variables were used to identify vegetation variables related to abundance levels of passerines, and to selected resident and migrant species for which model assumptions (i.e., normality) were met using 1992–93 data. The P value to remove a variable was 0.1 (SYSTAT Inc. 1992). To minimize problems associated with multicollinearity (Neter and Wasserman 1974), we used a minimum tolerance of 0.01 (SYSTAT Inc. 1992). All tests were considered significant at an alpha of ≤0.05.

RESULTS

A total of 21 passerine species was detected during the study (Table 1). Of these, 11 were residents and the rest temperate migrants. Blue Jays, Carolina Chickadees, Carolina Wrens, Ruby-crowned Kinglets, Northern Cardinals, and White-throated Sparrows were detected in greater numbers in levees than in swamps during both field seasons. Brown Thrashers, Rufous-sided Towhees and Hermit Thrushes were detected only in levees. Cedar Waxwings, Yellow-rumped Warblers and American Goldfinches were detected only in levees in 1992. Similarly, Eastern Phoebes and Eastern Bluebirds were detected only in swamps that year. Only the White-breasted Nuthatch had significantly greater abundance in swamps than in levees both seasons (Table 1).

Mean number of passerines in levees was significantly higher than in swamps each year (91–92: $t = 4.96$, df = 14; 92–93: $t = 4.60$, df = 43) (Table 2). We also detected significantly more resident species and temperate migrants in levees than in swamps each year. Within levees or swamps, we detected significantly more resident species than migrants in both years. In swamps, mean passerine counts were significantly greater in 1992–93 than in 1991–92 ($t = 4.74$, df = 27). Mean passerine counts did not differ significantly between years in levees.

Levees had significantly higher plant species richness, herbaceous cover, and stem density than swamps (Table 3). In contrast, swamps had significantly greater densities of pole (13–27 cm), small saw (28–37 cm), and large saw timber (≥38 cm). Passerine abundance, across both levees and swamps, varied significantly with levels of horizontal cover, plant richness, and negatively with small saw timber ($F = 16.60$, df = 3, 41). Within levees, abundance of passerines was significantly and positively related to levels of horizontal cover, whereas, in swamps, it was positively related to density of small saw timber and canopy cover (Table 4). The abundance of Carolina Chickadees in levees was positively related to density of seedling/saplings and pole timber; in swamps their abundance was negatively related to density of seedling/saplings. The abundance of Tufted Titmice and Carolina Wrens was primarily related to low vegetation components (e.g., horizontal cover, seedling/saplings) (Table 4). The abundance of the White-breasted Nuthatch was negatively related to density of pole timber in levees and positively to small saw timber in swamps. The abundance of Golden-crowned Kinglets was positively related to stems <2 cm diameter and seedling/saplings, both in levees and swamps, but negatively related to horizontal cover in swamps. Winter Wrens were negatively related to horizontal cover in levees and swamps, whereas, the

TABLE 1

MEAN DETECTIONS/STATION (± SE) AND BETWEEN VEGETATION COMMUNITY COMPARISONS OF OVERWINTERING RESIDENT AND TEMPERATE MIGRANT[a] SPECIES, ROANOKE RIVER, NORTH CAROLINA

Species	1991–1992		1992–1993	
	Levee	Swamp	Levee	Swamp
Eastern Phoebe (*Sayornis phoebe*)	0	0.05 ± 0.02	0.15 ± 0.03	0.25 ± 0.05
Blue Jay (*Cyanocitta cristata*)	0.19 ± 0.06	0	0.14 ± 0.06*	0.01 ± 0.01
Carolina Chickadee (*Parus carolinensis*)	1.11 ± 0.11*	0.41 ± 0.08	1.39 ± 0.10*	0.81 ± 0.09
Tufted Titmouse (*P. bicolor*)	0.35 ± 0.11	0.30 ± 0.07	0.67 ± 0.06*	0.41 ± 0.08
White-breasted Nuthatch (*Sitta carolinensis*)	0.28 ± 0.08	0.87 ± 0.03*	0.46 ± 0.07	1.71 ± 0.14*
Brown Creeper[a] (*Certhia americana*)	0.02 ± 0.01	0.06 ± 0.03	0.34 ± 0.02	0.06 ± 0.02
Carolina Wren (*Thryothorus ludovicianus*)	1.47 ± 0.09*	0.33 ± 0.04	1.88 ± 0.15*	0.71 ± 0.09
Winter Wren[a] (*Troglodytes troglodytes*)	0.14 ± 0.04	0.15 ± 0.05	0.32 ± 0.04	0.26 ± 0.05
Golden-crowned Kinglet[a] (*Regulus satrapa*)	0.08 ± 0.03	0.08 ± 0.04	0.25 ± 0.04	0.26 ± 0.05
Ruby-crowned Kinglet[a] (*R. calendula*)	0.27 ± 0.11	0	0.53 ± 0.06*	0.02 ± 0.01
Eastern Bluebird (*Sialia sialis*)	0	0.01 ± 0.01	0.04 ± 0.02	0.12 ± 0.05
Hermit Thrush[a] (*Catharus guttatus*)	0.04 ± 0.01	0	0.35 ± 0.08	0
American Robin[a] (*Turdus migratorius*)	0.81 ± 0.70	0	0.24 ± 0.06	0.15 ± 0.04
Brown Thrasher (*Toxostoma rufum*)	0.02 ± 0.02	0	0.01 ± 0.01	0
Cedar Waxwing[a] (*Bombycilla cedrorum*)	0.06 ± 0.04	0.01 ± 0.01	0.15 ± 0.09	0.05 ± 0.03
Yellow-rumped Warbler[a] (*Dendroica coronata*)	0.14 ± 0.05	0	0.18 ± 0.04	0.12 ± 0.03
Northern Cardinal (*Cardinalis cardinalis*)	0.33 ± 0.11*	0.01 ± 0.01	0.44 ± 0.10*	0.03 ± 0.02
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	0	0	0.05 ± 0.03	0
Fox Sparrow[a] (*Passerella iliaca*)	0.02 ± 0.02	0	0	0.01 ± 0.01
White-throated Sparrow[a] (*Zonotrichia albicollis*)	0.58 ± 0.11	0	0.20 ± 0.07*	0.01 ± 0.01

TABLE 1
CONTINUED

Species	1991–1992		1992–1993	
	Levee	Swamp	Levee	Swamp
American Goldfinch (*Carduelis tristis*)	0.14 ± 0.06	0	0.18 ± 0.04	0.08 ± 0.02

Asterisk indicates significant ($P < 0.05$) differences within years, *t*-tests.

abundance of Yellow-rumped Warblers was related to large saw timber in levees and negatively to canopy cover in swamps (Table 4).

DISCUSSION

Most passerine species, irrespective of their migratory status, were more abundant in natural levees than in swamps. Similar results were reported by Dickson (1974) and Kennedy (1977) for other bottomland forests in southeastern United States. Kennedy (1977) compared overwintering passerine abundance between swamps and forest tracks similar in plant composition to levees in our study. He reported significantly higher abundance for 8 of 11 species found to be significantly more abundant in levees in this study. Mean annual counts for passerines were significantly different in swamps, but not in levees. Determining the underlying causes for the observed interannual variability was beyond the scope of this study. Possible explanations include annual variations in population numbers, either locally or regionally; changes in habitat structure or food availability; or flood conditions. We measured and documented seasonal flood fluctuations in 1992–93, but they did not influence avian abundance fluctuations that year (Zeller 1994). We believe, however, that observer bias and differences in species detectability (Shields

TABLE 2
MEAN DETECTIONS/STATIONS (± SE) AND COMPARISONS BETWEEN VEGETATION COMMUNITY TYPES OF OVERWINTERING PASSERINE SPECIES ALONG THE ROANOKE RIVER, NORTH CAROLINA

Species group	1991–1992		1992–1993	
	Levee	Swamp	Levee	Swamp
Passerine community[a]	6.03 ± 0.66*	2.27 ± 0.19	7.68 ± 0.44*	5.07 ± 0.35
Resident species	3.88 ± 0.25*	1.98 ± 0.17	5.42 ± 0.31*	4.14 ± 0.29
Temperate migrant	2.15 ± 0.64*	0.29 ± 0.06	2.26 ± 0.20*	0.93 ± 0.12

[a] Passerine community does not include crows, grackles, cowbirds or starlings.
Asterisk indicates significant ($P < 0.05$) differences within years, *t*-tests.

Table 3

Comparisons of Winter Structural Variables (± SE) Between Natural Levee and Swamp Vegetation Communities along the Roanoke River, North Carolina

Structural variable	Levee	Swamp
Canopy height (m)	27.80 ± 0.56	26.33 ± 0.88
Canopy cover	0.78 ± 0.02	0.75 ± 0.02
Plant species richness (mean no. sp.)	17.50 ± 0.45*	7.80 ± 0.32
Horizontal cover (wood and herbaceous)	0.82 ± 0.04	0.75 ± 0.03
Woody cover	0.63 ± 0.05	0.73 ± 0.03
Herbaceous cover	0.19 ± 0.05*	0.02 ± 0.01
Stem counts (mean/0.04 ha)		
<2 cm diameter	125.46 ± 21.08*	11.66 ± 2.99
Seedlings/saplings (2–12 cm dbh)	12.96 ± 1.16	10.12 ± 2.21
Pole timber (13–27 cm dbh)	7.55 ± 0.48	11.46 ± 7.40*
Small saw timber (28–37 cm dbh)	3.04 ± 0.28	4.62 ± 0.63*
Large saw timber (≥38 cm dbh)	4.48 ± 0.17	10.63 ± 0.70*

Asterisk indicates a significant difference, *t*-tests ($P < 0.05$).

Table 4

Structural Variables Identified as Significant Predictors ($P < 0.05$) of Abundance for Overwintering Passerines and Selected Resident and Temperate Migrant Species[a] within Vegetation Communities along the Roanoke River, North Carolina (1992–1993)

	Levee		Swamp	
	Variable	r^2	Variable	r^2
Passerines	Horizontal cover	0.54	Canopy cover Small saw timber	0.46
Carolina Chickadee	Seedlings/saplings Pole timber	0.32	Seedlings/saplings*	0.17
Tufted Titmouse	Horizontal cover	0.16	Seedlings/saplings*	0.21
White-breasted Nuthatch	Pole timber*	0.20	Small saw timber	0.44
Carolina Wren	Horizontal cover Large saw timber*	0.27	Horizontal cover	0.31
Winter Wren[b]	Horizontal cover*	0.21	Horizontal cover*	0.11
Golden-crowned[b] Kinglet	Stem <2 cm diam. Seedlings/saplings	0.33	Horizontal cover* Stem <2 cm diam.	0.56
Yellow-rumped[b] Warbler	Large saw timber	0.16	Canopy cover*	0.22

[a] Asterisk indicates a significant negative relationship with abundance.
[b] Migrant species.

1979) were not determining factors influencing interannual variability in swamps because abundance levels in levees were similar between years and avian composition in both vegetation community types and years was the same.

Numerous authors have documented the relationship among plant species richness and structural diversity, and bird abundance (e.g., Recher 1969, Barrow 1990). In this study, variability in passerine abundance across vegetation community types was positively related to horizontal cover (index to understory structural complexity), higher plant species richness, and lower density of small saw timber. Low vegetation features (e.g., stems <2 cm, seedling/saplings) were prevalent in levees, where abundance levels were higher for most species. Within vegetation community types, understory and midstory components (e.g., horizontal cover, seedlings/saplings) accounted for significant proportions of the variability in abundance of nearly every selected species, except for the White-breasted Nuthatch and Yellow-rumped Warbler. The abundance of these species was better predicted by overstory components (e.g., saw timber). Vegetation components identified in our analyses are also among the substrates used during winter (e.g., foraging, resting) by the selected species (Hamel et al. 1982). For instance, Carolina and Winter Wrens are typically associated with mid- and understory vegetation. Vegetation components in these layers emerged as predictors of their abundance. White-breasted Nuthatches are associated primarily with the overstory layer. A major contributor to this layer is saw timber, a major component of swamps where nuthatches were significantly more abundant. Canopy cover, another predictor of abundance in the analyses, probably plays a role in providing protection from wind and precipitation (Morrison et al. 1986).

Hunter (in press) emphasized the need to redirect some conservation efforts towards resident species and temperate migrants, particularly in habitats experiencing high loss rates such as bottomland forests. Data on species-habitat relationships, such as those presented here, are necessary to begin to understand the causal relationships between vegetation changes on wintering grounds and breeding populations (see Petit et al. 1993). Avian conservation strategies in the Roanoke River Floodplain need to be formulated paying particular attention to silviculture and dam operations. We think that management practices outlined by Pashley and Barrow (1993) are adequate to maintain vegetation components identified in this study. Of major concern from a conservation perspective in the Roanoke is the altered and unpredictable flow regimes caused by flood control structures and power generating facilities (Schneider et al. 1989). Dam-regulated rivers could impact the availability of vegetation features

influencing abundance and distribution of overwintering passerines by affecting regeneration and species pioneering processes, as well as growth conditions (Sharitz and Lee 1985, Schneider and Sharitz 1986, Schneider et al. 1989). These studies suggest that, in the long-term, the Roanoke River's altered flooding regime is likely to create larger, less diverse areas of low elevation forest (i.e., swamps), which were found to attract fewer numbers of overwintering passerines. Due to the potential floodplain-wide effects on avian abundance and distribution, changes in vegetation structure as a function of altered flooding patterns need to be studied. Until more specific vegetation requirement data are available, we favor maintaining diverse vegetation communities in bottomland forests as recommended by Barrow (1990) and Pashley and Barrow (1993). This approach also accommodates the need to manage for year round avian vegetative requirements (i.e., breeding birds).

ACKNOWLEDGMENTS

We thank Donald H. White, Jerry Holloman, and J. Merrill Lynch for their support throughout the project. We also thank Cynthia Coffman, Tracey Elmeer, Susan Grove, Sharlene Krieger, Barbara Morrow, Lori Peoples, Michael Sanderson, and Judy Wood for their assistance in the field. We are grateful to the North Carolina Wildlife Resources Commission, The Nature Conservancy, U.S. Fish and Wildlife Service, National Biological Survey, and private land owners for funding the project and facilitating access to study areas. We thank Russ Lea, Kenneth H. Pollock, William H. Swallow, Jeffrey R. Walters, Michael L. Morrison, Danny Ingold, and W. James Fleming for reviewing earlier versions of this manuscript.

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WATERBIRDS, WETLANDS AND RECREATION: PUTTING SUSTAINABILITY INTO PRACTICE

An international conference jointly organized by British Ornithologists' Union & The Wildfowl & Wetlands Trust

Recreation on and around wetlands is now more widespread and intensive than ever before, to the extent that it is often the principal threat to their conservation value. Increasing human populations and/or affluence in many countries can only mean that this problem will increase. To achieve sustainability, recreational needs have to be integrated into the conservation of biodiversity. The aim of this international conference is to synthesize the current scientific understanding of the effects of recreational activities e.g., hunting, fishing, watersports and informal recreation) on wetlands, to formulate solutions to specific problems and to condsider how these may be consolidated within wider ecosystem management activities. In addition to the production of a scientific proceedings, the aim is to produce a practitioners guide to sustainable recreation on and around wetlands. The conference will be held at Wills Hall, Bristol, UK, from 19–21 April 1996. Offers of abstracts for posters and papers should not exceed 400 words and should be sent to: **Jeff Kirby, The Wildfowl & Wetlands Trust, Slimbridge, Gloucester, GL2 7BT, UK.** Booking enquiries should be sent to: **Graeme Greene, British Ornithologists' Union, % British Museum (Natural History), Subdepartment of Ornithology, Tring, Hertfordshire, HP23 6AP, UK.**

Wilson Bull., 107(4), 1995, pp. 709–718

CONTRIBUTIONS OF THE CONSERVATION RESERVE PROGRAM TO POPULATIONS OF BREEDING BIRDS IN NORTH DAKOTA

Douglas H. Johnson and Lawrence D. Igl

Abstract.—Previous studies have shown that habitat provided by the Conservation Reserve Program (CRP), a feature of the 1985 farm bill, is used by many birds. The present study quantitatively assesses the importance of the CRP by estimating changes in breeding-bird populations of North Dakota projected if CRP land would revert to cultivation. Of 18 species that were common in CRP or crop fields or both, 12 were more abundant in CRP habitats. Six of these species had suffered significant population declines during 1967–1990, according to the North American Breeding Bird Survey. In contrast, none of the six species that were more common in cropland than in CRP fields had declined significantly. Termination of the Conservation Reserve Program and a return of enrolled land to cultivation is projected to cause population declines in North Dakota exceeding 17% for Sedge Wren (*Cistothorus platensis*), Grasshopper Sparrow (*Ammodramus savannarum*), Savannah Sparrow (*Passerculus sandwichensis*), Dickcissel (*Spiza americana*), and Lark Bunting (*Calamospiza melanocorys*). *Received 27 October 1994, accepted 11 May 1995.*

The Conservation Reserve Program (CRP), established by the 1985 Food Security Act and administered by the U.S. Department of Agriculture, resulted in the reversion of millions of hectares of marginal cropland to perennial cover (Young and Osborn 1990). The primary objectives of the CRP were to bring crop supplies more in line with demands and to conserve soil and water resources. Certain highly erodible or eroding lands were removed from agricultural production, through 10-year contracts and annual payments, by establishing perennial vegetation. The intent was to reduce soil erosion, reduce sedimentation of streams, and thus improve water quality. Contracts begin to expire in the next few years, and most landowners indicated an intention to return their lands to cultivation (Mortensen et al. 1989, Kurzejeski et al. 1992).

A secondary objective of the CRP was to enhance habitat for fish and wildlife populations. Grassland habitats established by the CRP benefit a variety of wildlife species (King 1991, Luttschwager and Higgins 1992, Hall and Willig 1994), especially breeding birds (Johnson and Schwartz 1993a, b; Kantrud 1993). Populations of many grassland birds have declined in recent decades, especially in areas of intensive agriculture, such as the Midwest (Warner 1994) and the northern Great Plains (Johnson and Schwartz 1993b). Johnson and Schwartz (1993b) found that the two most common breeding-bird species observed in CRP fields in the north-

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ern Great Plains were Lark Bunting (scientific names are in Table 1) and Grasshopper Sparrow, species that showed declines in midcontinental Breeding Bird Surveys by about 60% during the previous quarter-century. Other declining grassland species such as Dickcissel, Clay-colored Sparrow, Baird's Sparrow, and Bobolink were also common in many CRP fields (Johnson and Schwartz 1993b).

The objective of this paper is to estimate the relative importance of the CRP to breeding populations of grassland birds in North Dakota. We determined the changes in bird populations expected if the land enrolled in CRP were returned to crop production. We used available data collected in 1992 and 1993 from two independent studies in North Dakota (1) surveys of statewide breeding-bird populations and (2) surveys of breeding birds in CRP fields.

STUDY AREAS AND METHODS

Statewide study.—The statewide study was a repeat of a survey originally conducted in 1967 of 130 legal quarter-sections (64.7 ha each), constituting a stratified random sample throughout the state of North Dakota (Stewart and Kantrud 1972). We did not receive permission to survey birds in two of the original quarter-sections, one in 1992 and another in 1993. The total area surveyed was 8335 ha in 1992 and 8332 ha in 1993.

We surveyed breeding birds using methods of Stewart and Kantrud (1972), which allow a fairly rapid assessment of breeding-bird communities in a field or quarter-section. Surveys were conducted by two observers on foot. (Sometimes only a single observer was available; he then covered the two halves in succession.) Each observer surveyed breeding birds on a rectangular half (805 × 402 m; 32.4 ha) of a quarter-section by following a standardized survey route. This route was 100 m inside of and parallel to the sides of the rectangle. We deviated up to 100 m from the route if necessary to adequately survey all habitats. We searched each quarter-section once or twice each year between late April and mid-July.

Surveys began about dawn and ended by midafternoon. Surveys extended beyond the time of most active bird vocalization, but Stewart and Kantrud (1972) concluded that activities of open-country birds were not appreciably affected by time of day other than early morning and late evening. We tallied all indicated breeding pairs, based on singing or calling males, females (for Brown-headed Cowbirds), observed pairs, or presence of an active nest. For individuals observed on the boundary of a plot, we credited the plot with 0.5 pair. We assigned breeding pairs to one of nine major habitat types, including cropland and CRP. We took care to avoid duplication in the counts and surveys under adverse weather conditions (precipitation or strong winds).

We estimated statewide breeding-bird populations, all habitats combined, by multiplying average densities by biogeographical stratum by the area each stratum made up, and summing across strata (Stewart and Kantrud 1972).

CRP study.—The CRP study is a continuing investigation that examines breeding-bird communities in CRP fields in nine counties in Minnesota, Montana, North Dakota, and South Dakota (Johnson and Schwartz 1993a, b). We restrict attention here to three North Dakota counties; Eddy, Kidder, and Hettinger, one in each of the major landforms of North Dakota that contain appreciable areas of CRP habitat (Johnson and Schwartz 1993a, b). We surveyed 132 fields totaling 2734 ha in 1992 and 145 fields totaling 3001 ha in 1993. In addition, several quarter-sections in the statewide study included CRP fields, which we used

Table 1

Densities of Breeding Birds (Number of Pairs per 100 ha) in North Dakota in CRP Fields and Crop Fields, 1992 and 1993, and Trends in Abundance Estimated from Midcontinental Breeding Bird Surveys (1967–1990)

Species	1992		1993		BBS trend[a]
	CRP	Crop	CRP	Crop	
Lark Bunting (*Calamospiza melanocorys*)	24.2	2.0	8.6	1.3	−4.22*
Grasshopper Sparrow (*Ammodramus savannarum*)	20.3	1.3	11.7	0.6	−4.58*
Red-winged Blackbird (*Agelaius phoeniceus*)	19.4	1.9	9.7	0.9	−0.04
Savannah Sparrow (*Passerculus sandwichensis*)	6.5	0.1	8.1	1.5	0.63
Western Meadowlark (*Sturnella neglecta*)	6.1	1.3	6.4	1.2	−0.32
Brown-headed Cowbird (*Molothrus ater*)	6.3	1.1	4.6	1.5	−0.26
Bobolink (*Dolichonyx oryzivorus*)	7.4	2.8	3.9	2.1	−2.74*
Clay-colored Sparrow (*Spizella pallida*)	4.5	0.0	4.0	0.0	−2.08*
Common Yellowthroat (*Geothlypis trichas*)	2.1	0.0	2.1	0.0	−0.32
Horned Lark (*Eremophila alpestris*)	2.2	20.1	1.0	29.1	0.15
Mourning Dove (*Zenaida macroura*)	1.8	1.7	0.9	1.6	−0.07
Sedge Wren (*Cistothorus platensis*)	1.0	0.0	1.5	0.0	−0.97
Vesper Sparrow (*Pooecetes gramineus*)	1.7	1.8	0.7	2.9	0.24
Baird's Sparrow (*Ammodramus bairdii*)	0.2	0.3	1.4	0.0	−2.58*
Dickcissel (*Spiza americana*)	1.5	0.2	0.1	0.0	−1.44*
Upland Sandpiper (*Bartramia longicauda*)	0.4	1.0	0.2	0.7	4.14*
Chestnut-collared Longspur (*Calcarius ornatus*)	0.3	1.4	0.2	2.1	−0.47
Killdeer (*Charadrius vociferus*)	0.1	1.1	0.0	1.2	0.25

[a] Asterisk indicates a significant ($P < 0.05$) trend.

to augment our samples of that habitat type. By doing so we added 11 CRP fields totaling 548 ha in both years.

In the northern Great Plains, most CRP land is planted to a mixture of grasses and legumes. Johnson and Schwartz (1993b) reported that most common species in North Dakota CRP fields included alfalfa (*Medicago sativa*), crested and other wheatgrasses (*Agropyron cristatum* and *A.* spp.), and smooth brome (*Bromus inermis*). Most CRP fields have remained relatively idle during the contract period, although some fields were released for emergency haying and grazing due to drought in several years and flooding in 1993. These disturbances took place after birds were surveyed each year.

We surveyed birds in CRP fields using the same methods as in the statewide study, except that a single observer surveyed small fields. We surveyed each field once each year between late May and early July. We computed densities of indicated breeding pairs for each species in CRP habitat. We projected these densities to the state by multiplying them by the total area of CRP in the state (1,287,133 ha). Implicit in this computation is the assumption that the fields we surveyed were representative of CRP fields throughout the state.

We also compared densities of breeding birds in CRP and in cropland. Cropland estimates were based on fields encountered in our statewide survey involving 4115 ha in 1992 and 4146 ha in 1993. To predict the consequences of the termination of the CRP and conversion of CRP fields to cropland, we substituted cropland densities for CRP densities into the values that made up statewide totals. This procedure assumes that all CRP fields would return to cultivation; about 15% of CRP contract holders in North Dakota surveyed indicated that they would retain permanent cover on their fields (Mortensen et al. 1989). Actual retention would depend on commodity prices and other dynamics of the agricultural marketplace.

Trends.—We obtained trends in abundance of grassland bird species from the Breeding Bird Survey (BBS) (Robbins et al. 1986) during 1967–1990 for the Central Region of North America between the Rocky Mountains and the Mississippi River (J. R. Sauer and B. G. Peterjohn, pers. commun.). Trends are based on statistical methods described by Geissler and Sauer (1990).

RESULTS

Of the 18 species that occurred commonly in CRP or cropland fields, 12 were more common in CRP fields than in cropland (Table 1). One, the Sedge Wren, occurred only in CRP. Six of the species that favored CRP habitat had suffered significant ($P < 0.1$) population declines; the Grasshopper Sparrow and Lark Bunting, for example, each declined by about two-thirds during 1967–1990. The Mourning Dove, an edge species, was nearly equally common in the two habitat types. Species more common in cropland than in CRP were Horned Lark, Vesper Sparrow, Upland Sandpiper, Chestnut-collared Longspur, and Killdeer, species that tend to avoid the taller and denser vegetation in CRP fields. None of those five species nor the Mourning Dove had exhibited population declines during 1967–90.

Estimated numbers of breeding pairs in CRP fields, and in all habitats, for North Dakota in 1992 and 1993 demonstrate the extensive use of CRP by many species (Table 2). CRP composed only about 7% of the land in North Dakota but supported more than 20% of the statewide population

TABLE 2
ESTIMATED NUMBERS OF BREEDING PAIRS (1000'S) STATEWIDE, IN CONSERVATION RESERVE PROGRAM FIELDS, AND PERCENTAGE, IN NORTH DAKOTA, 1992 AND 1993

Species	1992			1993		
	State	CRP	Percent	State	CRP	Percent
Lark Bunting	1540.6	311.0	20.2	686.1	110.8	16.1
Grasshopper Sparrow	889.7	261.2	29.4	1000.8	150.3	15.0
Red-winged Blackbird	1306.1	250.2	19.2	1535.6	124.4	8.1
Savannah Sparrow	294.6	83.5	28.4	595.9	104.1	17.5
Western Meadowlark	1079.5	78.2	7.2	1440.8	82.0	5.7
Brown-headed Cowbird	555.4	81.4	14.7	772.0	59.1	7.7
Bobolink	405.0	95.5	23.6	370.9	50.0	13.5
Clay-colored Sparrow	563.6	57.5	10.2	622.2	51.1	8.2
Common Yellowthroat	196.3	27.5	14.0	375.2	26.5	7.1
Horned Lark	2412.0	27.8	1.2	3671.6	12.3	0.3
Mourning Dove	741.6	23.7	3.2	732.7	11.4	1.6
Sedge Wren	43.1	12.5	29.1	19.2	79.7	24.1
Vesper Sparrow	479.1	21.2	4.4	843.8	8.7	1.0
Baird's Sparrow	170.7	3.1	1.8	278.7	17.6	6.3
Dickcissel	73.5	19.4	26.4	30.5	0.7	2.4
Upland Sandpiper	236.2	5.5	2.3	198.2	2.9	1.5
Chestnut-collared Longspur	1350.6	4.1	0.3	1707.4	2.2	0.1
Killdeer	247.9	1.2	0.5	311.8	0.4	0.1

of many species in one or both years. That percentage, averaged for the two years, was 26.6 for Sedge Wren, 22.9 for Savannah Sparrow, and 22.2 for Grasshopper Sparrow. At the other extreme, CRP supported only about 2.7% of Vesper Sparrows and 0.7% of Horned Larks in the state.

If we assume the return of CRP habitat to cropland and substitute densities of breeding birds in cropland for densities in CRP, we obtain a measure of the importance of CRP to each species (Table 3). Conversion of CRP to cropland would have reduced numbers of Sedge Wrens by 25.8%, Grasshopper Sparrows by 20.5%, and Savannah Sparrows by 18.8%. Conversely, numbers of Horned Larks and Vesper Sparrows would have risen by 9.7% and 2.3%, respectively.

DISCUSSION

Previous studies have shown that many bird species benefit from grassland habitats established by the CRP (Burger et al. 1990; King 1991; Luttschwager and Higgins 1992; Johnson and Schwartz 1993a, b; Kantrud 1993; Patterson 1994; Reynolds et al. 1994). We found that CRP fields are especially important for grassland birds during the breeding season,

TABLE 3

ESTIMATED NUMBER OF BREEDING PAIRS (1000's) OF BIRDS IN CRP FIELDS IN NORTH DAKOTA, ESTIMATED NUMBER IF CRP WERE CROPLAND, PREDICTED CHANGE IN BREEDING PAIRS, STATEWIDE NUMBER OF BREEDING PAIRS, AND PREDICTED CHANGE AS PERCENTAGE OF STATEWIDE POPULATION, MEAN VALUES FOR 1992–1993

Species	Population in		Change	Statewide population	Percent change
	CRP	Crop			
Lark Bunting	210.9	21.2	−189.7	1113.4	−17.0
Grasshopper Sparrow	205.7	12.4	−193.4	945.2	−20.5
Red-winged Blackbird	187.3	17.8	−169.5	1420.9	−11.9
Savannah Sparrow	93.8	10.2	−83.6	445.2	−18.8
Western Meadowlark	80.1	15.8	−64.4	1260.2	−5.1
Brown-headed Cowbird	70.2	17.1	−53.1	663.7	−8.0
Bobolink	72.8	31.2	−41.6	387.9	10.7
Clay-colored Sparrow	54.3	0.3	−54.0	592.9	−9.1
Common Yellowthroat	27.0	0.3	−26.7	285.8	−9.3
Horned Lark	20.1	316.2	296.1	3041.8	9.7
Mourning Dove	17.6	21.6	4.0	737.1	0.5
Sedge Wren	15.8	0.0	−15.8	61.4	−25.8
Vesper Sparrow	15.0	30.2	15.2	661.4	2.3
Baird's Sparrow	10.4	2.3	−8.0	224.7	−3.6
Dickcissel	10.1	1.2	−8.9	52.0	−17.1
Upland Sandpiper	4.2	10.1	5.9	217.2	2.7
Chestnut-collared Longspur	3.1	22.3	19.1	1529.0	1.3
Killdeer	0.8	14.5	13.7	279.8	4.9

including Sedge Wrens, Grasshopper Sparrows, Savannah Sparrows, Dickcissels, Lark Buntings, Red-winged Blackbirds, Common Yellowthroats, Clay-colored Sparrows, and Bobolinks. Six of these species had suffered appreciable declines between 1967, when Breeding Bird Surveys began in the region, and 1990.

Declines in grassland bird populations have been attributed to a number of causes, including the loss of suitable nesting habitat on the breeding grounds. The vast grasslands that once dominated the landscape in the northern Great Plains are largely gone or degraded (Samson and Knopf 1994). Recent analysis of BBS data indicates that some species that were declining in North Dakota before the CRP began (i.e., 1967–1986), such as the Grasshopper Sparrow and the Lark Bunting, have shown population increases coincident with the establishment of perennial grasslands after the CRP began (i.e., 1987–1992) (Reynolds et al. 1994). These results, in combination with our findings, suggest that the CRP provides not only important breeding habitat for some grassland birds but also a possible vehicle for restoring abundant populations of these species.

Most of the species more common in cropland than in CRP fields select the sparser cover that cropland affords (e.g., Graber and Graber [1963] and Stewart [1975] for Killdeer; Owens and Myres [1973] and Skinner [1975] for Horned Lark; Owens and Myres [1973] for Chestnut-collared Longspur; Wiens [1969], Owens and Myres [1973], and Rodenhouse and Best [1983] for Vesper Sparrow). Conversely, the Upland Sandpiper frequently forages in sparse cover (Graber and Graber 1963) but prefers to nest in somewhat more robust vegetation (Kantrud and Higgins 1992, Bowen and Kruse 1993). Higher densities of Upland Sandpipers found in cropland may reflect use primarily for foraging, and CRP fields may offer nesting habitat that is otherwise limited in highly cultivated or heavily grazed areas of the northern Great Plains.

Although the comparisons we made apply to North Dakota, the implications extend to other areas in the northern Great Plains. Currently, there are nearly 4 million ha enrolled in CRP in the northern Great Plains (Montana, Minnesota, North Dakota, and South Dakota), which accounts for nearly one-quarter of the total land in the CRP nationwide (Johnson et al. 1994).

Recent evidence suggests that CRP also benefits grassland bird populations in other areas of intensive agriculture such as the Midwest. In Nebraska, King (1991) found 16 species of birds in CRP fields and 13 species in native prairie during the breeding season, compared with only two species, Horned Lark and Killdeer, in cropland. Likewise, in Iowa, Patterson (1994) found 16 species of birds nesting in CRP fields compared with only two species, Horned Lark and Vesper Sparrow, in similar areas of cropland. Our data indicate that the addition of CRP habitat in the North Dakota landscape reduced numbers of a few species, such as Horned Larks and Vesper Sparrows, species whose populations had not declined in the last quarter-century.

Some breeding birds were undoubtedly missed in our single survey (e.g., Järvinen and Lokki 1978). The same techniques were used in both surveys, however, so any bias should be consistent. Because estimates of population size are minimal, projections of population change anticipated from termination of CRP are conservative. Projections also assume habitat-specific densities of species and that densities in one habitat will not change dramatically in response to changes in the availability of another. This simplifying assumption is necessary and probably adequate as long-term averages. The year-to-year variability evident in the densities of birds (Table 2) also points to the need to consider averages over long periods of time.

Our projections are based on the assumption that all CRP fields would be returned to cultivation. Some small fraction would likely be retained

in perennial vegetation and used for grazing or forage production (Mortensen et al. 1989). Such habitat would support different bird populations from cropland, but probably lower numbers than CRP habitat maintains.

Although we did not examine reproductive success, it seems reasonable that birds are more successful in robust and undisturbed cover than they would be in crop fields, most of which are cultivated, sprayed, or otherwise disturbed frequently during the breeding season (e.g., Best 1986). For several waterfowl species, Kantrud (1993) and Reynolds et al. (1994) found that nest success in CRP fields was as high or higher than in habitats specifically purchased and managed for waterfowl production.

The Conservation Reserve Program is an agricultural commodities program and is inherently expensive. As such, it does not compete with programs to conserve habitat for wildlife. The primary benefits of CRP include major reductions in soil erosion in the Great Plains; from 1987 to 1992 North Dakota croplands experienced a 68% reduction in erosion from wind and a 22% reduction in erosion from water (USDA 1994). CRP does, however, offer far greater benefits to breeding birds and other wildlife populations than do other agricultural programs such as annual set-asides and summer fallow.

ACKNOWLEDGMENTS

We appreciate the cooperation of the numerous land owners and operators who allowed us access to their property, to the state Agricultural Stabilization and Conservation Service (ASCS) directors, and to the executive directors and staffs of county ASCS offices who kindly provided us with information on CRP fields. J. R. Sauer of the National Biological Service and B. G. Peterjohn of the U.S. Fish and Wildlife Service supplied information from the Breeding Bird Survey. We thank C. J. Johnson, R. L. Manson, M. D. Schwartz, C. M. Shoemaker, and K. A. Ward for their assistance in the field. J. A. Grzybowski, H. A. Kantrud, R. R. Koford, D. L. Larson, and J. L. Zimmerman provided constructive comments on the manuscript.

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ERRATUM

In "Diet of nesting killdeer in North Dakota" by Jeanne M. Fair, Patricia L. Kennedy and Lowell C. McEwen (Wilson Bull. 107:174–178) one incorrect line occurs in the text. The second line in the last paragraph should read "Orthoptera *availability* fell within the Bonferonni 95% confidence interval for the expected proportion, Coleoptera was lower than the confidence interval, and other arthropods were above the interval.

Wilson Bull., 107(4), 1995, pp. 719–723

SHORT COMMUNICATIONS

Birds of coniferous forest on Mount Graham, Arizona.—Because of interest in the effect upon the biota of Mount Graham by current development for astronomy, I repeated observations and censuses made there forty years ago. Avifaunal changes have occurred. Unlike my companion study in the Sierra Nevada (Marshall 1988), the losses at Mount Graham of nesting species—all at the lower altitudinal limit of *Pinus leiophylla chihuahuana* and *P. ponderosa arizonica*—lack an obvious connection to human interference with the environment.

Study area.—Mount Graham, in southeastern Arizona, is capped with old growth Engelmann spruce and alpine fir from 3000 m to the summit at 3267 m. This boreal forest of 8 km^2 is at its southernmost limits on the North American continent. Descending, one passes through other vegetation zones in sequence: Douglas firs and white firs mixed with spruce, and then mixed with Mexican white pines; south slopes of New Mexican locust and Gambel oak; ponderosa pine with Gambel oak; ponderosa pine mixed with silver-leaf oak; and finally Chihuahua pine with Arizona oak (Martin and Fletcher 1943, Hoffmeister 1956, Marshall 1957, Mohlenbrock 1987). From memory, notes, and photographs I detect no change in vegetation during the forty-year study period. Specifically, the trees at the mapped census area in Wet Canyon (Fig. 1) have not closed ranks about the little openings suitable for those foothill birds that forage among grasses, boulders, manzanitas, and nolinas.

The mesic luxuriance of Mount Graham's vegetation is shown by running streams supporting tall groves of maples, by the enormous Douglas firs that remain, by the profusion of understory flowers and green forbs, and by the gigantic stature of clear-trunked alders dominating Wet Canyon. Martin and Fletcher (1943) underestimated rainfall because they lacked gauge readings from comparable north slopes elsewhere in the state.

The bird-life of Mount Graham was partly analyzed from studies of a wider area by Henshaw (1875), Monson (1937), and Marshall (1957). This is the first complete documentation of birds that spend the summer in coniferous forest there. Other birds using Mount Graham forests in summer are early fall and late spring (well into June) migrants—species whose breeding range is set forth in the two state ornithologies (Phillips et al. 1964, Monson and Phillips 1981).

The 794.5 ha of boreal (Hudsonian) forest of alpine fir with Engelmann spruce is in one continuous tract, all but 23.5 ha of it enclosed within the 1229 ha fenced-off astrophysical area. I was not permitted to enter in 1991, but I did see tree-cutting, road-building, trucks hauling earth down to the foot of the mountain, and students looking for red squirrels (*Tamiasciurus grahamensis*). Other human activity included heavy logging until recently and a road-building scheme (prisoner road, Fig. 1), mercifully called off. The forest on the north slope was all cut, but the east slope appears natural.

Methods.—My field notes and census maps of summer resident birds found within coniferous forest at Mount Graham are deposited in the library of the Division of Birds, Smithsonian Institution. They document the identifications, occurrences, numbers, and activities of the birds. Actual dates of field censusing from 1949 to 1953 are in Marshall (1957). In 1991 I revisited the sites shown (Fig. 1) from 4 to 5 June and 17 to 18 July 1986, 17 to 19 and 21 to 23 June 1991. Gale Monson was my companion on the first 1991 visit, Tom Huels on the second. I examined all of H. W. Henshaw's and E. G. Holt's Mount Graham specimens in the Smithsonian Institution, and those of other collectors in the Western Foundation of Vertebrate Zoology, Louisiana State Univ., and Univ. of Arizona. Species

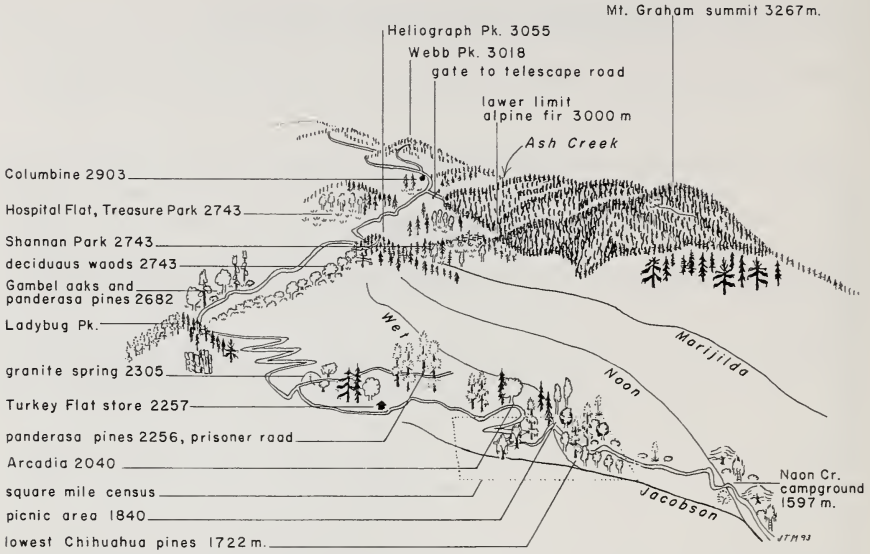

FIG. 1. Mount Graham from the east, showing altitude and characteristic vegetation of the places searched for birds.

represented by those specimens, which I identified to subspecies, are indicated by an asterisk in the results. My stereo tape recordings of 1986 and 1991, which confirm many identifications, are at the Univ. of Florida.

Results.—On 5 July 1951 I counted these numbers of pairs, flocks, or singing males along 3.1 km of trail through alpine fir and Engelmann spruce forest from a point on the south ridge of Mount Graham to the summit: Red-tailed Hawk (*Buteo jamaicensis**) 1, Band-tailed Pigeon (*Columba fasciata**) flock plus scattered individuals, Broad-tailed Hummingbird (*Selasphorus platycercus**) 12, Hairy Woodpecker (*Picoides villosus**) 8, Northern Flicker (*Colaptes auratus cafer**) 2, Cordilleran Flycatcher (*Empidonax occidentalis**) 7, Violet-green Swallow (*Tachycineta thalassina**) 1 group, Steller's Jay (*Cyanocitta stelleri diademata**) 4, Common Raven (*Corvus corax*) 1, Mountain Chickadee (*Parus gambeli**) 25, Red-breasted Nuthatch (*Sitta canadensis**) 6, Pygmy Nuthatch (*Sitta pygmaea**) 10, Brown Creeper (*Certhia americana**) 12, Golden-crowned Kinglet (*Regulus satrapa**) 12, Ruby-crowned Kinglet (*R. calendula**) 2, Hermit Thrush (*Catharus guttatus auduboni**) 25, American Robin (*Turdus migratorius**) 3, Yellow-rumped Warbler (*Dendroica coronata auduboni**) 20, Western Tanager (*Piranga ludoviciana**) 3, Yellow-eyed Junco (*Junco phaeonotus**) 12, Red Crossbill (*Loxia curvirostra bendirei**) flock of 12 plus scattered individuals, and Pine Siskin (*Carduelis pinus**) 2. I found most of them occupying the lower coniferous zones too, in decreasing abundance. Additional abundant species that I found mainly in the pine zones are the Turkey Vulture (*Cathartes aura*), Zone-tailed Hawk (*Buteo albonotatus*), Wild Turkey (*Meleagris gallopavo,* not seen 1986, 1991), Flammulated Owl (*Otus flammeolus*), Whip-poor-will (*Caprimulgus vociferus arizonae*), Solitary Vireo (*Vireo solitarius plumbeus*), Warbling Vireo (*Vireo gilvus**), Virginia's Warbler (*Vermivora virginiae**), Hepatic Tanager (*Piranga flava**), and Black-headed Grosbeak (*Pheucticus melanocephalus**). All but the turkey are as numerous today as they were in the early 1950s.

I heard or saw few Cooper's Hawk (*Accipiter cooperii**), Northern Goshawk (*Accipiter*

gentilis), Northern Pygmy-Owl (*Glaucidium gnoma*), Northern Saw-whet Owl (*Aegolius acadicus*), Acorn Woodpecker (*Melanerpes formicivorus*), Ruby-crowned Kinglet, Red-faced Warbler (*Cardellina rubrifrons**), and Pine Siskin. Greater Pewee (*Contopus pertinax**), American Dipper (*Cinclus mexicanus**), Western Bluebird (*Sialia mexicana**), Orange-crowned Warbler (*Vermivora celata**), and Olive Warbler (*Peucedramus taeniatus**) were not found.

The Spotted Owl (*Strix occidentalis*), Magnificent Hummingbird (*Eugenes fulgens**), White-breasted Nuthatch (*Sitta carolinensis**), House Wren (*Troglodytes aedon brunneicollis**), and Grace's Warbler (*Dendroica graciae*) have increased dramatically since the 1950s. The Painted Redstart (*Myioborus pictus**) has decreased.

The remaining results deal with losses or reductions at my 132 ha census plot in Wet Canyon (not all of the 259 mapped ha of the square shown in Fig. 1 being accessible). For each species I add the number of pairs or singing males from my census of 1951 in all habitats—the various combinations of pines, riparian trees, evergreen oaks, and manzanita bushes. I found no flycatchers other than the abundant and ubiquitous Cordilleran Flycatcher after 1953 (except that I heard one Western Wood-Pewee, *Contopus sordidulus,* in 1986). The Western Wood-Pewee 11, Dusky-capped Flycatcher (*Myiarchus tuberculifer*) 8, Ash-throated Flycatcher (*Myiarchus cinerascens*) 3, and Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*) 2 were gone.

These oak woodland species were missing in 1986 and 1991: Western Screech-Owl (*Otus kennicottii aikeni**, specimen 1960) 2, Elf Owl (*Micrathene whitneyi*) 5, Common Poorwill (*Phalaenoptilus nuttallii**) 3, Black-chinned Hummingbird (*Archilochus alexandri**) 7, Strickland's Woodpecker (*Picoides stricklandi arizonae*) 1, Bridled Titmouse (*Parus wollweberi**) 5 and a flock, Bushtit (*Psaltriparus minimus*) 4 and a flock of 30, Canyon Wren (*Catherpes mexicanus**) 2 in 1952, Rufous-crowned Sparrow (*Aimophila ruficeps*) 5 and present in 1986, and Scott's Oriole (*Icterus parisorum*) 2. Although those species have probably just contracted their range into oak and riparian woodland at a lower altitude, the Bridled Titmouse is the only one that Tom Huels and I could find in oaks at Noon Creek campground (Fig. 1) in June 1991. Contrastingly, these denizens of the same habitat, the Scrub Jay (*Aphelocoma caerulescens woodhouseii**), Gray-breasted Jay (*Aphelocoma ultramarina**), Bewick's Wren (*Thryomanes bewickii**), Blue-gray Gnatcatcher (*Polioptila caerulea*), Hutton's Vireo (*Vireo huttoni**), Black-thoated Gray Warbler (*Dendroica nigrescens**), and Rufous-sided Towhee (*Pipilo erythrophthalmus**) have stood their ground in Wet Canyon.

Discussion.—The House Wren is the champion of change on Mount Graham. H. W. Henshaw's specimen of 1874 (Frontispiece) is the subspecies *brunneicollis,* the four of E. G. Holt in 1914 are grayish *parkmanii,* and all adults that Tom Huels and I saw close in strong sunlight in 1991 are *brunneicollis,* a field-identifiable subspecies (but see Marshall 1956) now an abundant summer resident everywhere on the mountain at least as far down as the willows at Noon Creek crossing. But in the 1950s it was rare and of unknown subspecies. Aside from two territories at the bottom of Wet Canyon in 1951, one of which was occupied in 1952, my only records are, for 1951: "29 June, Heliograph Peak, one singing at tower, one edge of meadow lower. 7 July, south slope of Heliograph Peak, 9000 feet, one singing in deciduous woodland."

The Red Crossbill also switched taxa from *stricklandi* in 1874* to *bendirei* in 1951*, 1966*, 1986*, and 1991*. Mexican, giant *stricklandi* now inhabits the neighboring Chiricahua Mountains, whereas the juveniles with single cranial layer show that *bendirei* nested on Mount Graham in 1991.

In 1949 to 1953 I searched for Spotted Owls all over Mount Graham and had no difficulty in finding them in neighboring southern Arizona mountains during that period. Therefore I

feel it safe to say that they were absent from Mount Graham (or else sequestered on the remote north slope). The first record was by Dave Steadman (field notes deposited at New York State Museum, Albany), who heard one on 28 September 1979 in fir forest at Hospital Flat and on 30 September 1979 another in spruce forest of Webb Peak. My first encounter was on 18 June 1991, when Gale Monson and I listened to a male that called all night from the east face above the prisoner road (CD).

No evidence from my studies on other mountaintops of southern Arizona (Marshall 1957, Phillips et al. 1964) explains the dearth of Greater Pewees, American Dippers, Western Bluebirds, Orange-crowned Warblers, and Olive Warblers. All had been collected by Henshaw or Holt, although the pewees were from September and Henshaw classed them as migrants.

No bird species to my knowledge is confined to the alpine firs inside the astrophysical area. Assuming that the entire area is not developed, those birds common in 1951 should persist. They were all abundant in lower coniferous zones in 1991. The four species of flycatchers are rare or gone altogether. Because their breeding habitat in the Pinaleno Mountains is pristine and unchanged, there must be destruction of vegetation where birds from these particular summer colonies maintained their winter territories (Marshall 1988). Wade C. Sherbrooke (in litt.) and Helen Snyder (in litt.) report normal numbers of these flycatchers for the Chiricahua Mountains in the 1991 season, as does Sheri Williamson (in litt.) for the Huachuca Mountains.

Acknowledgments.—I thank Gale Monson, Tom Huels, and Thomas Waddell for their assistance and advice in the field; David W. Steadman for providing full documentation of his Spotted Owl record; Tom Huels, Jeff Groth, and Allan R. Phillips for assistance in my study of crossbills; Helen Myslicki and Sally Monson for their hospitality in Tucson; the John Simon Guggenheim Memorial Foundation for its support of field work in the summers of 1951 to 1953; and the Univ. of Arizona for sponsoring my trips to Mount Graham.

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Wilson Bull., 107(4), 1995, pp. 723–727

Seasonal and diurnal mass variation in Black-capped Chickadees and White-throated Sparrows.—During the winters of 1989–90 and 1990–91, we recorded mass of free-ranging Black-capped Chickadees (*Parus atricapillus*) and White-throated Sparrows (*Zonotrichia albicollis*) in northern New Jersey. The data presented here are the first records of seasonal and diurnal mass variation for untrapped passerines in North America. Previous studies have shown that captivity and handling can significantly bias results of studies of avian mass (King and Farner 1966, Castro et al. 1991, Refsnider 1993).

Study area and methods.—We recorded mass of Black-capped Chickadees in Mendham, New Jersey (40°46′N, 74°32′W) from November 1990 through March 1991. We weighed White-throated Sparrows from January through March in 1990 and 1991. The study site was in a residential suburban neighborhood containing several feeders. Local weather conditions during the two winters of observation were milder than usual with less than normal precipitation (National Climatic Data Center 1989–91).

We initially captured birds in mist nets or wire traps and marked them with USF&W bands and a unique combination of colored plastic leg bands. The birds were released within 30 min at the site of capture. Periodically throughout the winter season, we recorded body mass as birds alighted on the platform of a baited electronic digital balance that had an accuracy of 0.1 g and an operating temperature range of −5°C to +35°C. We recorded mass during three periods of the day (1)"AM" (sunrise minus 30 min to sunrise plus 2 h), (2) "Midday" (11:00–13:00 EST) and (3) "PM" (sunset minus 2 h to sunset plus 30 min). The balance was connected by cable to a personal computer inside the building. During a bird's visit, 20 consecutive readings at 0.4-sec intervals were recorded. We included only those weight measurements judged to be stable or those that met the following criteria (1) if, within the list of weights recorded during a single visit, there was a minimum of three consecutive weights that differed by no more than 0.1 g, the mean of the consecutive weights was accepted as the body mass during that visit, or (2) if no such group of three existed, the mean of four or more consecutive weights was accepted, so long as none of the values differed by more than 0.2 g (twice the sensitivity of the balance) from the mean. For the AM period the earliest mass recorded was selected for analysis, for the midday period the mass recorded nearest 12:00 was chosen, and for the PM period the latest recorded mass was selected.

We analyzed the data using SAS (1985) procedures in order to generate descriptive statistics. We tested for the reduction in variance explained when comparisons were made between linear and quadratic regression analyses (Steel and Torrie 1960). We used correlation coefficients to test significance of linear regression models. We used goodness of fit,

R, and *F*-comparison tests as measures of significance for reduction of variance due to the X^2-term of the quadratic.

Results.—The two species in the study differed in their pattern of seasonal mass variation (Fig. 1). Black-capped Chickadee maintained a relatively stable mass over the winter. Data for White-throated Sparrow demonstrate a significant ($P < 0.01$) linear decrease in mass from midwinter to spring. As chickadees did not visit the experimental platform during most of January 1991, we distinguished between data collected during the early period, November through December 1990, and the later period, February through March 1991. A test for unequal observations and unequal variances indicated that midday data for these two calendar periods were not homogeneously distributed; however, mean mass was not significantly different: 1990 = 11.4 g vs 1991 = 11.5 g; $F_{78,26} = 1.40$; $P > 0.05$. We analyzed chickadee data for the two periods separately prior to pooling, and found that coefficients of variation were 4.1% and 4.8% respectively, suggesting a stable seasonal pattern in this species.

Black-capped Chickadees and White-throated Sparrows differed with respect to their patterns of diurnal variation (Table 1, Fig. 2). For Black-capped Chickadee, pooled data for the entire winter of 1990–91, based on equal variances for all individuals, indicate significant ($P < 0.05$) mass gain between each diurnal period, followed by overnight mass loss. For White-throated Sparrow, pooled data indicate a significant ($P < 0.05$) gain in mass only between the AM and the midday periods.

Discussion.—Pooled data for the Black-capped Chickadees show minimal mass variation over the winter. These results differ from those of Haftorn (1989) who showed mass variation of several species of free-ranging Paridae in Norway conformed to a pattern of winter fattening in which daily mass amplitude varies seasonally and morning mass tends to increase in winter. Our data are similar to those of Lawrence (1958) who showed over five winters that seasonal mass for repeatedly trapped resident Black-capped Chickadees in Ontario varied relatively little. Lawrence quantified seasonal mass variation for Black-capped Chickadee by computing the average of the differences between the lowest and highest mass over the winter expressed as percent of the lowest weight. Using this procedure for our midday data, we computed a seasonal variation for Black-capped Chickadee of 6.7% (range: 5.3–9.2%; N = 6). Lawrence's data, which do not specify time of weighing, show a seasonal mass variation of 7.3% (range: 5–12%; N = 28). Lawrence's data for migrant Black-capped Chickadees show greater mass variation over the season (11.1%; range 8–17%; N = 17).

We note that the robustness of our data suffers from the paucity of records in January due to the infrequency of feeding activity by Black-capped Chickadees at the weighing apparatus during that month. Without a good record for January, the possibility of a departure from the stable seasonal mass pattern for chickadee during that period cannot be ruled out. However, if a seasonal peak in mass were to occur in January, it would have to be of relatively rapid onset and decline. Haftorn's (1989) findings that the mass of most of the birds he studied increased gradually toward a midwinter peak would argue against the probability of a sudden sharp peak occurring in January for Black-capped Chickadee.

Our data are consistent with Rogers and Smith's (1993) conclusion that species of an avian tree-foraging guild employ a winter survival strategy that minimizes variation in body mass, while species of a ground-foraging guild exhibit an increase of mass in midwinter in harsh climates. The tree-foraging Black-capped Chickadee showed relatively little mass variation over the season compared with that shown by the ground-foraging White-throated Sparrow.

Diurnal mass variation data for Black-capped Chickadee in this study are similar to those published by Haftorn (1989) for Paridae in Norway and Howitz (1981) for Black-capped Chickadee in Minnesota. The birds in all three studies gained mass gradually over the day. The pattern of diurnal mass increase shown for White-throated Sparrow in the present study

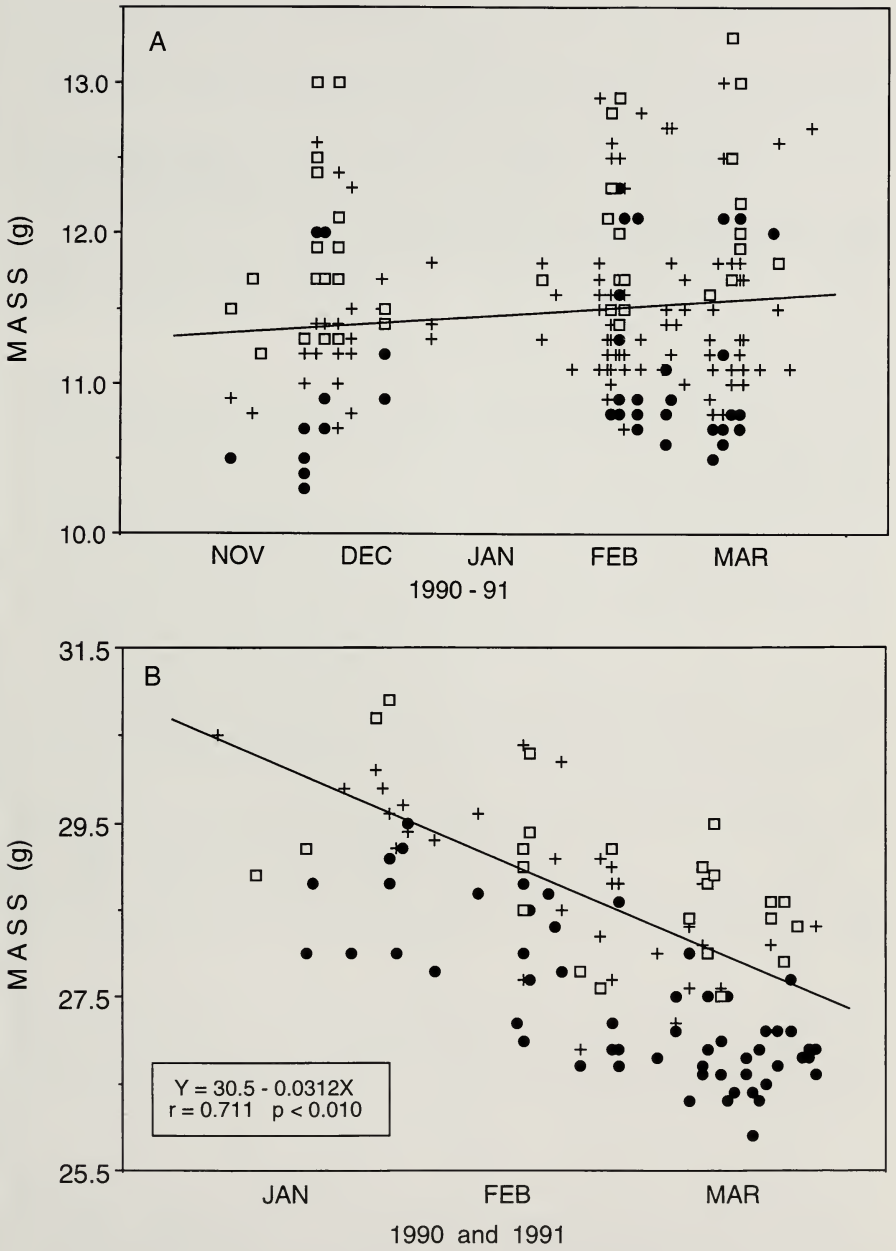

FIG. 1. Mean mass (g ± SE) for Black-capped Chickadee (A) and White-throated Sparrow (B). Best fit lines are for midday data; regression for chickadee was not statistically significant. AM mass (solid circle), midday mass (crossbar), PM mass (open square).

Table 1

Diurnal Mass Change for Black-capped Chickadee and White-throated Sparrow over Three Periods of the Day

	AM		Midday		PM		Percent change in mass[a]		
	N	Mass g (SE)	N	Mass g (SE)	N	Mass g (SE)	AM-MID	MID-PM	PM-AM
Black-capped Chickadee (pooled data for 6 individuals)									
Early[b]	11	10.9 (0.2)	27	11.4 (0.1)	19	11.8 (0.1)	4.3%	3.7%	−8.2%
Late[c]	28	11.1 (0.1)	79	11.5 (0.1)	22	12.0 (0.1)	3.6%	4.6%	−8.4%
Season	39	11.1 (0.1)	106	11.5 (0.1)	41	11.9 (0.1)[e]	3.8%	3.9%	−7.9%
White-throated Sparrow (pooled data for 3 individuals)									
Season[d]	58	27.4 (0.1)	33	28.8 (0.2)	24	28.9 (0.2)[e]	5.2%	0.1%	−5.4%

[a] Percent change in mean mass for each period based on the earlier mass.
[b] 13 Nov.–30 Dec. 1990.
[c] 25 Jan.–24 Mar. 1991.
[d] 01 Jan.–30 Mar. 1990 and 01 Jan.–30 Mar. 1991.
[e] Separate underlined data are significantly different at $P < 0.05$, multiple comparison test.

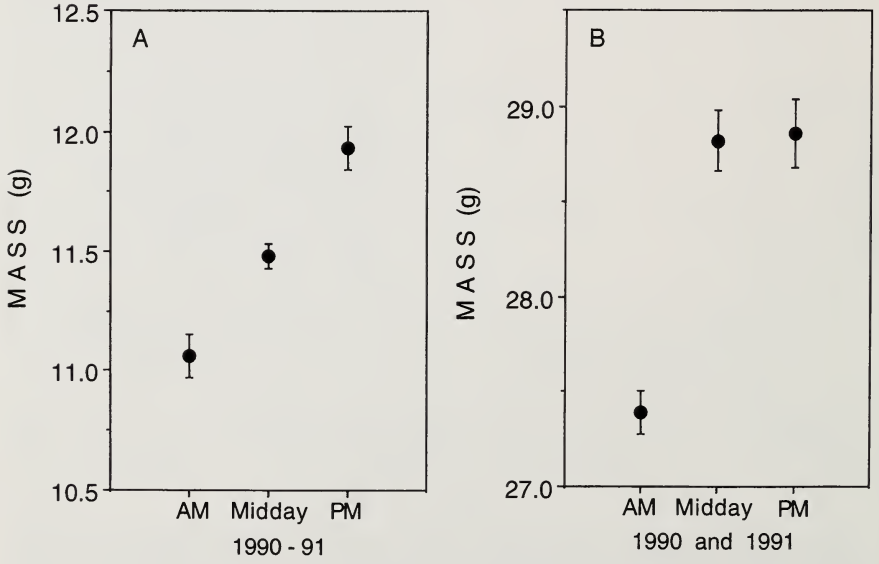

Fig. 2. Mean mass (g ± SE) for Black-capped Chickadee (A) and White-throated Sparrow (B) for three periods of the day.

is consistent with Kontogiannis' (1967) finding that captive birds of this species showed maximum rate of increase in mass during the first 2.5 hours of the day.

Black-capped Chickadee-RWR, the dominant female, gained, on average, nearly twice as much mass over the course of the day in comparison to the dominant male RBR (1.08g vs 0.62 g, representing an average daily change of 9.6% vs 5.6%). RBR exhibited the smallest daily amplitude of mass variation, suggesting that being the dominant male may facilitate energy conservation in roosting.

Acknowledgments.—We are indebted to Mary Doscher for instruction in banding technique, John Fennimore for apparatus modification, and Douglas White, Charles Leck, Richard Kane, Paul Kerlinger, Bertram Murray, Thomas Graedel and three anonymous reviewers for valuable technical and editorial advice.

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Wilson Bull., 107(4), 1995, pp. 727–733

Detectability and population density of Scaly-naped Pigeons before and after Hurricane Hugo in Puerto Rico and Vieques Island.—Detectability and density of Scaly-naped Pigeons before and after Hurricane Hugo hit northeastern Puerto Rico with sustained winds of 30–40 m/s (gusting from 50–60 m/s) on 18 September 1989 (see Boose et al.

1994). With the exception of some protected vegetation pockets, forest habitats along the coastline and in the mountains were devastated. Unprotected forests were completely stripped of leaves and fruits. As a result, some canopy and ground-dwelling frugivore/seedeater bird populations were severely impacted both directly and indirectly by the hurricane (Waide 1991; but also see Askins and Ewert 1991, Wauer and Wunderle 1992, Wiley and Wunderle 1993). This large-scale perturbation provided the opportunity of studying the resiliency of columbid populations under prolonged environmental stress (e.g., cover and food limitations).

Elsewhere I reported that Puerto Rican columbid populations sampled in September and October 1989 did not differ significantly from those sampled during the same time in 1986–87, and that increased detectability following the hurricane may have biased the counts since individuals and flocks were more visible when searching for food and cover in less affected areas (Rivera-Milán 1990a).

Here I provide data on the status of Scaly-naped Pigeon (*Columba squamosa*) nesting populations, and examine changes in the detectability and density of the species before and after Hurricane Hugo hit Puerto Rico and Vieques Island (1986–92). Roadside counts should be adjusted for detectability in different habitats, especially when vegetation cover condtitions change drastically as a result of defoliation (Rotella and Ratti 1986, Raphael 1987). Moreover, roadside counts are not necessarily reliable indicators of short-term changes in the size and success of nesting populations at local scales (Baskett 1993, and references therein). Therefore, I combined fixed- and unfixed-radius point counts along secondary and tertiary roads and strip-transect nest-counts to assess the effect of Hurricane Hugo on Scaly-naped Pigeon nesting populations in Puerto Rico and on Vieques Island.

The Scaly-naped Pigeon is an arboreal frugivore with a diverse diet (Pérez-Rivera 1978). The species is common in mesic habitats on the Puerto Rican mainland, and in xeric habitats on Vieques and Culebra islands (Rivera-Milán 1990b, 1992, 1993). It is the second most important game species of Puerto Rico (Rivera-Milán et al. 1990), hence accurate abundance estimates are needed to monitor population changes and guide management actions to maintain sustainable populations.

Study sites and methods.—Pre- and post-hurricane roadside counts were conducted in nine 8 km routes in the wet and moist zones of the Puerto Rican mainland (September–October 1986–89, and May 1987–92; Fig. 1 and Table 1). In May 1991–92, three routes with variable lengths were sampled in the dry zone of Vieques Island (Fig. 1 and Table 1). Vieques Island is the largest offshore territory (167 km^2) and lies 9.7 km from the Puerto Rican mainland (8903 km^2).

Six permanent stations at 1.6-km intervals were sampled/route on the Puerto Rican mainland. Because of the length of available secondary and tertiary roads, stations were at 0.8 km intervals on Vieques Island (four stations along road 995, six stations in Camp García and along Road 997, and ten stations inside the Naval Base Storage Facility). Call- and sight-counts were conducted for three minutes at each station in Puerto Rico and on Vieques Island from 06:00–10:30 AST (see Rivera-Milán 1993).

Detectability ($\hat{C}$) and density ($\hat{D}$) estimates were obtained from the combination of unfixed- and fixed-radius point counts (radius [r] = 60 m) at each station. Aural and visual detections outside the fixed area of the stations (πr^2) were used as supplementary data to estimate a species-specific constant to approximate the distance at which detectability dropped to zero. Detectability was estimated as $\hat{C} = 1 - (1 - P)^{0.5}/r$, where P equaled the number of detections inside 60 m (i.e., fixed count) divided by the number of detections inside and outside 60 m (i.e., unfixed count). Density was estimated as $\hat{D} = 3(10^6)N\hat{C}^2/\pi$, where N equaled the number of detections inside 60 m. The constant 10^6 was used to express $\hat{D}$ in km^2 (see Järvinen and Väisänen 1975, Järvinen 1978).

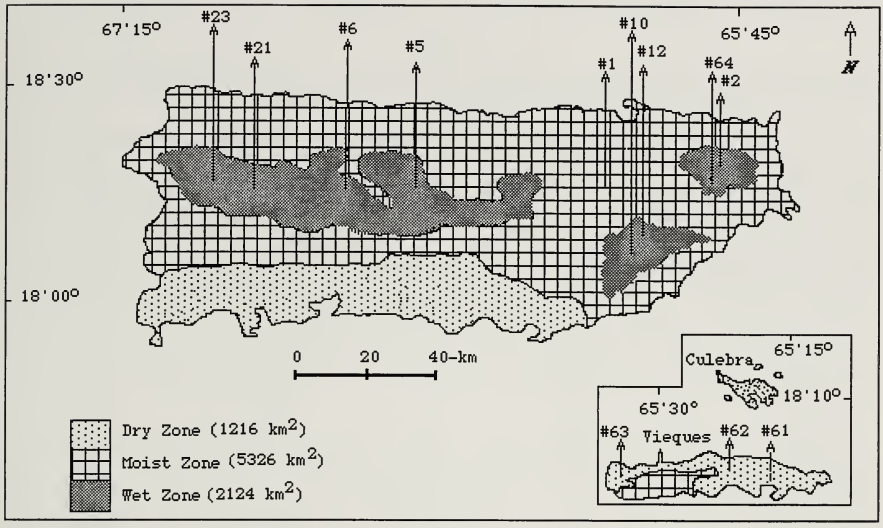

FIG. 1. Study sites and the three major life zones on Puerto Rico and its two major offshore territories, Vieques and Culebra islands.

TABLE 1

ROUTES USED TO EVALUATE THE EFFECT OF HURRICANE HUGO ON SCALY-NAPED PIGEON POPULATIONS

Location[a]	Habitat type
Puerto Rico	
Cidra	Moist montane forest
Luquillo	Rain forest
Barranquitas	Wet montane forest
Ciales	Wet montane forest
Cayey	Wet montane forest
Cayey	Wet montane forest
Adjuntas	Wet montane forest
Maricao	Wet montane forest
Naguabo	Rain forest and wet montane forest
Vieques Island	
Camp García and Road 997	Dry coastal forest
Road 995	Dry interior forest
Naval Base Storage Facility	Dry coastal forest

[a] See Fig. 1.

TABLE 2

DETECTABILITY ($\hat{C}$) AND DENSITY ($\hat{D}$) ESTIMATES OF SCALY-NAPED PIGEONS BEFORE AND AFTER HURRICANE HUGO IN PUERTO RICO AND ON VIEQUES ISLAND[a]

Date	Unfixed counts	Fixed counts	$\hat{C}$	$\hat{D}$
Puerto Rico				
Sept–Oct, 1986	22	7	0.00295	58.2
Sept–Oct, 1987	16	4	0.00223	19.0
Sept–Oct, 1989	18	8	0.00424	137.3
May, 1987	44	6	0.00118	8.0
May, 1988	60	13	0.00192	45.6
May, 1989	74	13	0.00154	29.2
May, 1990	101	27	0.00240	148.6
May, 1991	55	11	0.00176	32.5
May, 1992	60	12	0.00176	35.4
Vieques Island				
May, 1991	21	7	0.00306	62.5
May, 1992	16	6	0.00349	69.8

[a] $\hat{C}$ and $\hat{D}$ estimates were obtained from 72 km sampled in Puerto Rico and 15.2 km sampled on Vieques Island (see Methods).

Nest counts were conducted in 32 0.1-ha (10 × 100 m) strip-transects in Cidra and Cayey (Fig. 1: #1 and #12) from May–June 1987–92. A total of 314 transects were sampled on Vieques Island in May–June 1989; 344 were sampled in May–June 1990; and 52 in May–June 1991–92 (Fig. 1: #61–63). The habitat types sampled in Cidra and Cayey were second-growth montane forests characteristic of the moist and wet zones of Puerto Rico; whereas the habitat types sampled on Vieques Island were characteristic of coastal and interior dry forests (see Ewel and Whitmore 1973). Forests of Cidra and Cayey were little impacted by Hurricane Hugo unlike those of Vieques Island, which were damaged severely.

Wilcoxon's signed-rank test, which is the nonparametric equivalent of a two group paired *t*-test, was used to compare pre- and post-hurricane changes in detectability (significance $P \leq 0.05$).

Results.—Detectability ($\hat{C}$) of Scaly-naped Pigeons was higher immediately after (Sept.–Oct., 1989) than before (Sept.–Oct., 1986–87) Hurricane Hugo (z corrected for ties = −2.383, $P = 0.017$; z corrected for ties = −2.585, $P = 0.009$; Table 2). As a result, density ($\hat{D}$) estimates obtained from the combination of fixed- and unfixed-radius point counts along roads were higher immediately after than before the hurricane (Table 2). The detectability of Scaly-naped Pigeons in May 1990 did not differ significantly from that of May 1987–89 and 1991–92 on the Puerto Rican mainland (Wilcoxon's signed-rank tests, $P > 0.05$; Table 2). Detectability approached average levels in May 1990 (wet zone [1986–88]: mean $\hat{C}$ = 0.00132, SE = 0.00041, N = 24; 95% CI = 0.0005–0.00214; Rivera-Milán 1990b); and it returned to pre-hurricane levels in May 1991–92 (Table 2).

Detectability of Scaly-naped Pigeons in May 1991–92 (combined) on Vieques Island was significantly higher than that in May 1987 and 1989 on the Puerto Rican mainland (z corrected for ties = −1.997, $P = 0.046$; z corrected for ties = −2.201, $P = 0.028$); whereas

the other years (May 1988, 1990–92) did not differ significantly (Wilcoxon's signed-rank tests, $P > 0.05$; Table 2).

Scaly-naped Pigeons were not detected nesting on Vieques Island in May–June, 1990. But nesting populations rebounded to pre-hurricane levels after one year in Cidra and Cayey (low effect areas), and after two years on Vieques Island (high effect areas; Fig. 2A–C).

Discussion.—Detectability ($\hat{C}$) and density ($\hat{D}$) estimates increased as a result of Scaly-naped Pigeons being more visible when dispersing from high to low effect areas in search of cover and food. In Sept.–Oct. 1989, I observed 50–75 Scaly-naped Pigeons feeding at ground-level on fallen seagrapes (*Coccoloba uvifera*) on Culebra Island. Similarly, I observed flocks of 10–25 pigeons feeding on fallen fruits of yellow prickly-ash (*Zanthoxylum monophyllum*) and shortleaf fig (*Ficus laevigata*) on Vieques Island. I did not observe Scaly-naped Pigeons feeding on the ground on the Puerto Rican mainland; but flocks of 10–20 pigeons were seen feeding at canopy-level on fruits of Puerto Rican royal palm (*Roystonea boringuena*), trumpet tree (*Cecropia schreberiana*), and matchwood (*Didymopanax morototoni*).

In Sept.–Oct. 1989, I also saw flocks of 3–15 Scaly-naped Pigeons flying from Culebra and Vieques islands to the northeastern corner of the Puerto Rican mainland. From 1986–92, I did not observe Scaly-naped Pigeons moving from Puerto Rico to Culebra or Vieques islands. They were seen moving from Vieques Island to Puerto Rico before Hurricane Hugo, but mostly as singles or flying couples; their flocking behavior appeared to be more conspicuous immediately after the hurricane. The increase in density in Sept.–Oct. 1989 and May 1990 reflected in part an increase in the detectability of Scaly-naped Pigeons moving from high to low effect areas in Puerto Rico and on Vieques Island. That pigeons from Culebra and Vieques islands dispersed to Puerto Rico after the hurricane mainly in search of food and cover is supported by the lack of nesting activity found in May–June 1990 (the peak of the nesting season; Rivera-Milán 1990b) on Vieques Island. Nesting populations rebounded to pre-hurricane levels after one year in low effect areas on the Puerto Rican mainland, and after two years in high effect areas on Vieques Island. Scaly-naped Pigeon populations in the moist and wet zones of the Puerto Rican mainland increased slightly from May–June 1987–92. The density increase detected in May 1990 was followed by an increase in the number of active nests of Scaly-naped Pigeons in May 1991–92 (Table 2 and Fig. 2A–C). This appeared to be a response of the populations to a year of below normal reproduction (1990) in Puerto Rico and on Vieques Island.

The combination of unfixed- and fixed-radius point counts ("simple" vs "adjusted"; Raphael 1987) helped to account for changes in the detectability of Scaly-naped Pigeons before and after Hurricane Hugo. The unfixed and fixed roadside counts of Scaly-naped Pigeons were probably biased high on the Puerto Rican mainland in Sept.–Oct. 1989 and in May 1990, and on Vieques Island in May 1991–92. Detectability was higher immediately after (1989–90) than before (1987–88) the hurricane, because of the drastic loss of vegetation cover at canopy-level and the increased visibility of dispersing and foraging Scaly-naped Pigeons (Wiley and Wunderle 1993; J. M. Wunderle, unpubl. data).

Management decisions about the sustainability of nesting populations (e.g., reopening of the hunting season [September–November] on Vieques Island; Rivera-Milán et al. 1990) should be guided by standardized monitoring efforts. The combination of fixed- and unfixed-radius point counts along secondary and tertiary roads and strip-transect nest-counts facilitated the examination of changes in the size of Scaly-naped Pigeon nesting populations at local scales before and after Hurricane Hugo.

Acknowledgments.—I thank A. Ortiz, D. Ramos, E. Ramos, and A. Matos for spending many hours afield. F. Schaffner, J. Wiley, J. Wunderle, and two anonymous reviewers helped me to improve a previous version of the manuscript. This study was supported by Pittman-

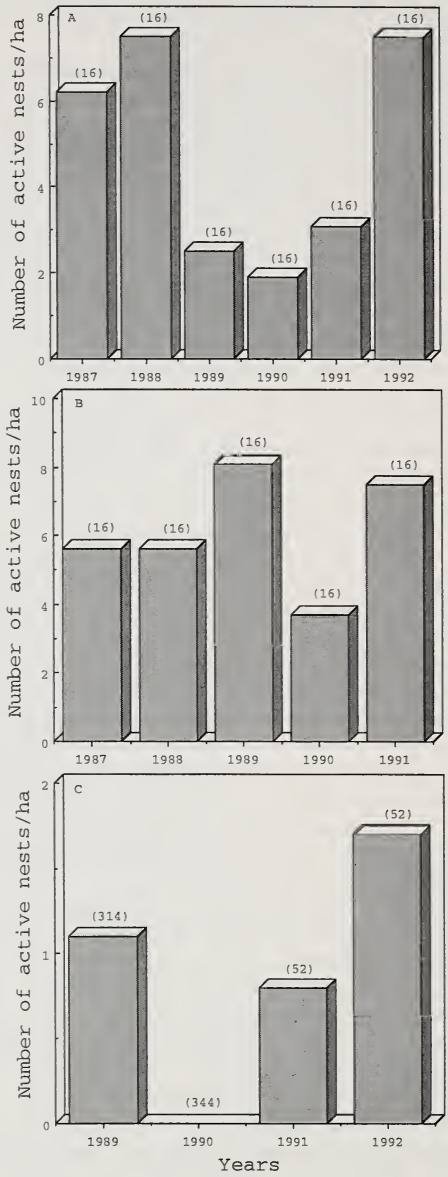

FIG. 2. Nesting density of Scaly-naped Pigeons before and after Hurricane Hugo in Cidra (A), Cayey (B), and on Vieques Island (C). Numbers in parentheses correspond to the number of 0.1-ha strip-transects sampled before and after the hurricane.

Robertson Funds grant-in-aid to the Terrestrial Ecology Section, Scientific Research Area, Puerto Rico Dept. of Natural Resources.

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Wilson Bull., 107(4), 1995, pp. 734–738

Botfly ectoparasitism of the Brown Cacholote and the Firewood-gatherer.—Flies of the genus *Philornis* (Diptera, Muscidae) are obligate subcutaneous parasites of birds (Pont 1972, Harwood and James 1987). Philornid botflies place their eggs on birds, generally chicks. The larvae burrow into the chick's skin and feed on its blood and body fluids (Uhazy and Arendt 1986). Mature larvae emerge through apertures in the skin producing large cutaneous lesion and posterior scars (Arendt 1985a, Uhazy and Arendt 1986). Pupation occurs on the bottom of the nest (Pont 1972). Lethality of fly parasitism depends on various factors such as age and size of nestlings, implantation sites, intensity of infestation, brood size, the amount of food that adults can bring to the nest, rainfall, and the thermal environment of the nest (Arendt 1985a, b, Mason 1985). Botfly parasitism has been documented in several Neotropical birds (Dinelli 1941; García 1952; Dodge 1968; Smith 1968; Pont 1972; Hector 1982; Fraga 1984; Arendt 1985a,b; Mason 1985; Young 1993). In this note, I report the prevalence and intensity of larvae in nestlings of the Brown Cacholote (*Pseudoseisura lophotes*) and the Firewood-gatherer (*Anumbius annumbi*), their infestation sites, and host mortality. I also report the simultaneous infestation by two species of *Philornis*.

Study area and methods.—I studied botflies in Monte Cristo (31°23′S, 63°53′W), Córdoba, Argentina, over a 4-yr period (1989–1993). Mean annual rainfall at study area is 790 mm, occurring briefly between November and March and the mean annual temperature is 16.5°C. I examined 144 Brown Cacholote nestlings in 67 clutches and 160 Firewood-gatherer nestlings in 50, and 211 and 189 adults, respectively, to determine the presence of botfly larvae. Adult and nestlings were marked individually with leg bands of colored plastic.

I removed 31 larvae from two Cacholote nestlings and 28 from three Firewood-gatherer nestlings, which were not included in the overall analyses. These larvae were reared in separate vials containing some stick as a substrate at ambient temperature. I preserved a sample of three larvae from each host species and the remainder allowed to form pupae, five of which were preserved. Forty-eight adult flies emerged and were preserved. S. Abalos of the Centro de Investigaciones Entomológicas de Córdoba identified philornid flies to species according to descriptions by Shannon and del Ponte (1927) and García (1952) descriptions.

Following Margolis et al. (1982), Fraga (1984), and Arendt (1985b), I measured (1) *prevalence* (percentage infested) among broods and nestlings, (2) *intensity* (number of larvae per infested host), and (3) *mortality* (number of dead nestlings per infested nestlings). I used a Chi-square test to compare fledging success (nestlings surviving from hatching to fledgling) between parasitized and unparasitized nestlings. To correlate annual rainfall with prevalence in nestling I used Spearman correlation. To correlate monthly rainfall with infestation rates I used a regression analysis.

Results.—Two different philornid species were found, *Philornis pici* and *P. seguyi*. The mean density was 11.1 larvae/Brown Cacholote's nestling (range: 3–21) and 8.8 larvae/Firewood-gatherer's nestling (range: 3–17). All of the nestlings of infested brood were parasitized. Hatchlings and young nestlings (one week old) were significantly more infested than older ones ($\bar{x}$ = 12 larvae vs 7.9 larvae; ANOVA, $F_{2,65} = 4.6$, $P < 0.05$).

Botfly parasitism caused the death of eight Brown Cacholote (30.7%) and nine Firewood-gatherer nestlings (31%), corresponding to 5.5% (8/144) and 5.6% (9/160) of total nestlings, respectively (Table 1). No significant difference was found in fledgling success in parasitized cacholotes (69%) and unparasitized ones (74.81%) (Chi-square test = 0.22, df = 1, $P > 0.5$) and in parasitized Firewood-gatherers (69.2%) and unparasitized ones (73.7%) (Chi-square test = 0.4, df = 1, $P > 0.5$).

Both species of botflies simultaneously occurred in nestlings of these two bird species.

TABLE 1

PREVALENCE OF BOTFLY INFESTATIONS IN BROWN CACHOLOTE AND FIREWOOD-GATHERER NESTLINGS IN MONTE CRISTO, 1989–1993

Species	Prevalence in broods (a)	%	Prevalence in nestlings (b)	%	Mortality N	%
Brown Cacholote	11/67	16.4	26/144	18	8	30.7
Firewood-gatherer	9/50	18	29/160	18.1	9	31

[a] Number of parasitized broods/total broods.
[b] Number of parasitized nestlings/total nestlings.

These larvae were at various stages in each nestling. In both species, the botfly larvae infested most body surfaces, especially on the head, throat, wings, legs and near the cloaca. There were no significant differences in some specific sites and the distribution of larvae did no vary with the nestling development.

The Brown Cacholote's reproductive period is longer (late September–February) (Nores and Nores 1994) than that of the Firewood-gatherer (September–December) (Nores and Nores unpubl. data). The rate of infestation by botfly larvae on nestling Cacholotes varied over the breeding season, peaking during November and decreasing during December. There were a few cases in October and January, and none in February (Fig. 1A). Infestation rates on nestling Firewood-gatherers did not vary over the breeding season (Fig. 1B). Botfly infestation varied among years in Brown Cacholote and Firewood-gatherer nestlings (Fig. 2), and was related to annual rainfall (Spearman rank $r^s = 0.97$, $P < 0.05$, and $r^s = 0.95$, $P < 0.05$, respectively). During the third (1991–1992) breeding season only one cacholote's brood was lightly parasitized (three to five larvae per nestling). During the study this was the driest year (670 mm). The most intense infestation in both species occurred in 1989–1990. During this wetter period (900 mm), mean intensity was 15 larvae/Brown Cacholote nestling (N = 11) and 13 larvae/Firewood-gatherer nestling (N = 13). I found no correlation between monthly rainfall and botfly infestation in Brown Cacholote nestlings ($r^2 = 0.55$, N = 24, $P > 0.05$) and in Firewood-gatherers ($r^2 = 0.35$, N = 16, $P > 0.05$.) None of the

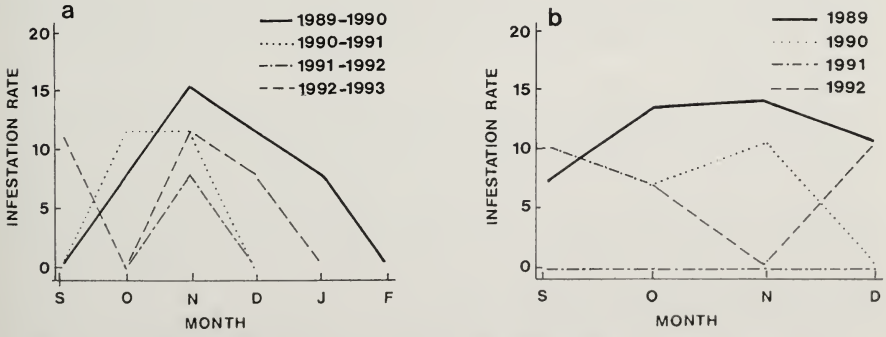

FIG. 1. Infestation rate during four breeding periods in Monte Cristo, (a) Brown Cacholote nestlings, (b) Firewood-gatherer nestlings.

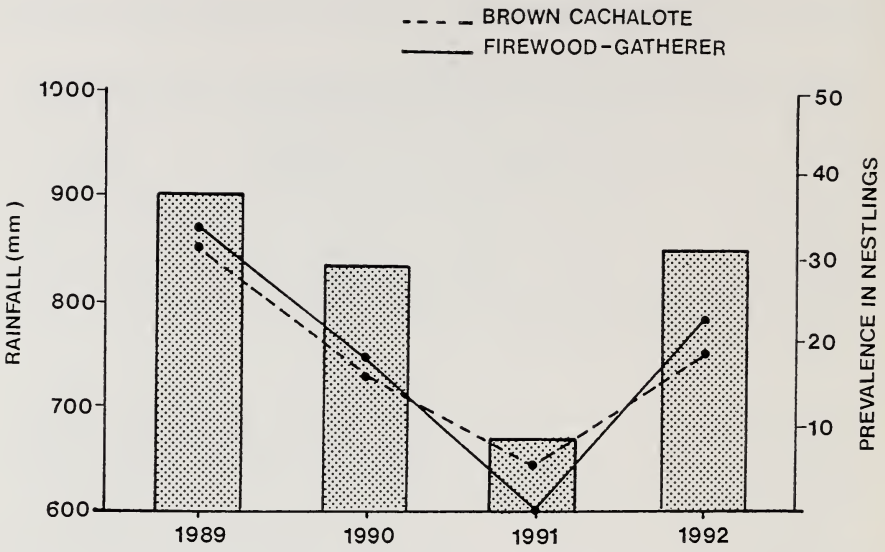

FIG. 2. Relationship between infestation of nestlings in Brown Cacholote and Firewood-gatherer and annual rainfall in Monte Cristo (1989–1993).

sampled adult birds of either species (211 Brown Cacholotes and 189 Firewood-gatherers) was infested during the study period.

Discussion.—Prevalence of botfly larvae in brood and nestlings was similar in both host species. Comparable values in nestlings on the Firewood-gatherer were observed by Fraga (1984) who found 33.3% and 18.2%, respectively. Mason (1985) recorded a brood prevalence of 32.5%. Their areas were slightly wetter (annual rainfall was about 1000 mm) than mine. Arendt (1985b) found that 96 percent of 448 nestling Pearly-eyed Thrashers (*Margarops fuscatus*) examined were infested and overall mean intensity was 37 larvae/nestling (range 0–220). In his study area the annual rainfall varies from 3000 mm to more than 5000 mm. I agree with him that infestation by botflies is associated with rainfall.

Hatchlings and young nestlings were more susceptible to infestation than older ones, because they were naked and less active. Philornid larvae were observed on all body surfaces of the nestling and no significant difference was found in any specific site and with the nestling's ontogeny.

Lethal infestation was more than 14 larvae per nestling in both species, but there were two exceptions. Two recently hatched Firewood-gatherer nestlings with four and six larvae, respectively, died, while a Brown Cacholote nestling fledged with 15 larvae.

Other birds species died with fewer larvae. Smith (1968) suggested that seven larvae were sufficient to kill nestlings of the Giant Cowbird (*Scaphidura oryzivora*) three species of oropendolas, *Zarrhinchus wagleri, Psarocolius decumanus, Gymnostinops montezuma* and one species of cacique, *Cacicus cela.* Mason (1985) reported a lethal intensity of six botfly larvae in eight species of passerine birds. Arendt (1985b) reported mortality in hatchling Pearly-eyed Thrashers infested with 1-5 larvae.

Thirty-one percent of the infested Firewood-gatherer nestlings and 30.7% of Brown Cacholote nestlings died. Fraga (1984) and Mason (1985) observed higher mortality rates (50%) in the Firewood-gatherer.

Some adult birds remove botfly larvae. Bay-winged Cowbirds (*Molothrus badius*) remove larvae from their nestlings and those of their brood parasite, the Screaming Cowbirds (*M. rufoaxillaris*) (Fraga 1984). Giant Cowbirds (*Scaphidura oryzivora*) remove botfly eggs and larvae from their own bodies and those from their host (Smith 1968). This behavior was not observed in the Brown Cacholote or the Firewood-gatherer.

Botfly ectoparasitism in adult birds has been documented for several species (García 1952, Dodge 1968, Arendt 1985b), but in this study, no adult Brown Cacholotes or Firewood-gatherers were parasitized by botfly larvae. *Philornis* ectoparasitism occurred fairly commonly at the nestlings, but it contributed slightly to total mortality (5.5% and 5.6%). It does not appear to be severe enough to affect population levels of these species.

Acknowledgments.—I sincerely thank my thesis advisor, M. Nores for his continued help and encouragement throughout my study. I thank W. Arendt and D. Forrester for helpful comments on the manuscript. I also thank J. Navarro for helping during data analysis. The Consejo de Investigaciones Científicas y Tecnológicas de la Provincia de Córdoba and the Consejo Nacional de Investigaciones Científicas y Técnicas provided founds through post-graduate scholarships.

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Wilson Bull., 107(4), 1995, pp. 738–741

Seasonal response of Wood Thrushes to taped-playback songs.—Broadcast vocalizations are a useful technique to detect various bird species (see review by Johnson et al. 1981), such as raptors (e.g., Lynch and Smith 1984, Kimmel and Yahner 1990, Morrell et al. 1991), marsh birds (e.g., Marion et al. 1981, Johnson and Dinsmore 1986, Kaufmann 1988), and songbirds (e.g., Falls 1981, Richards 1981). As part of a study focusing on nest-site selection and nesting success of Wood Thrushes (*Hylocichla mustelina*) in a forest managed for Ruffed Grouse (*Bonasa umbellus*) habitat in central Pennsylvania, we developed a survey protocol using taped-playback songs as a means of increasing the number of contacts of Wood Thrushes during the breeding season. Our objective in this study was to test the response of Wood Thrushes to taped-playback songs among three trials (I–III) during the 1992 and 1993 breeding seasons.

Study area and methods.—We conducted our study at the 1166-ha Barrens Grouse Habitat Management Area (HMA), State Game Lands 176, Centre County, Pennsylvania, from June–July in 1992 and 1993 (details of the Barrens Grouse HMA were given in Yahner 1993). The study area has been managed for Ruffed Grouse habitat since 1975 by the Pennsylvania Game Commission (PGC) using an even-aged system of forest clearcutting. The Barrens Grouse HMA consisted of a reference (control) and a treated (clearcut) sector of similar size. The PGC established four parallel transects on each of the two sectors to survey Ruffed Grouse populations at the Barrens Grouse HMA (Yahner 1984). Each transect was 3.2 km long and was oriented in an approximate N-S direction; distance between transects was 0.4 km.

We established 128 stations (N = 64/sector) at 200-m intervals along the eight transects. In both 1992 and 1993, each station was visited once per trial (early to mid-June, mid- to late June, and early to mid-July; trials I–III, respectively) between sunrise and 11:00 hr; the order of visits to transects was alternated between the two sectors. At each station, the observer recorded unsolicited contacts (sightings, call notes, songs) of Wood Thrushes during a 1-min equilibrium period (protocol modified from Morrell et al. 1991). A series of taped-playback songs (Cornell Laboratory of Ornithology, Cornell Univ.) of a Wood Thrush then was broadcasted, using a Johnny Stewart Bird and Animal Caller (Model MS512, Johnny Stewart, Waco, Texas). The series consisted of six songs, each separated by 10-sec pauses; the speaker was rotated to a different direction for each song. After the equilibrium and broadcast periods, the observer noted solicited contacts of Wood Thrushes during a 4-min post-broadcast period. Because of possible difficulty in an observer hearing Wood Thrushes during the playbacks, contacts noted only between the end of the pre-broadcast and before the post-broadcast period were not recorded. To minimize counting the same individual bird twice, contacts of birds recorded in the post-broadcast period included only

those believed to be of birds not seen or heard in the previous equilibrium period. When an unsolicited or solicited contact of a Wood Thrush was noted, period (equilibrium or post-broadcast), trial (I–III), and location of the bird were recorded.

The observed versus expected numbers of survey stations in which unsolicited contacts were noted in the 1-min equilibrium period were analyzed among the three trials (I–III) using *G*-tests for goodness-of-fit (Sokal and Rohlf 1981). Similarly, the observed versus expected number of survey stations in which solicited contacts were noted in the 4-min post-broadcast period were compared among the three trials. The expected number of stations per trial in both analyses was based on the sum of the observed number of stations in which contacts were recorded per trial divided by three trials. If the observed versus expected number of stations with contacts varied significantly ($P < 0.05$) among the three trials in either period, we used a posteriori *G*-tests for goodness-of-fit about the cell (trial) of interest (Sokal and Rohlf 1981).

Results.—Five-hundred eight contacts of Wood Thrushes were noted during the 1992 and 1993 breeding seasons combined. These included 247 (48.6%) unsolicited contacts at 91 stations in the equilibrium period and 261 (51.4%) solicited contacts at 99 stations in the post-broadcast period. The number of different Wood Thrushes seen or heard per visit to an individual station in both the equilibrium and the post-broadcast periods ranged from one to three. During the equilibrium period, one bird was recorded on 76.9%, two birds on 19.5%, and three birds on 3.6% of the total visits to the survey stations in which Wood Thrushes were noted. During the post-broadcast period, one additional bird was recorded on 73.0%, two additional birds on 20.9%, and three additional birds on 6.1% of the total visits to the stations in which thrushes were noted.

The number of stations at which at least one unsolicited contact of a Wood Thrush was recorded during the equilibrium period varied from expected among the three trials in 1992 and 1993 combined ($G = 7.96$, df = 2, $P < 0.05$) (Fig. 1). In trial I, the number of stations characterized by contacts of Wood Thrushes (N = 46, 18.0%) combined was less than expected ($G = 7.51$, df = 1, $P < 0.01$). In trials II and III, however, the number of stations in which Wood Thrushes were noted (N = 76 of total, 29.7%, and N = 68, 26.6%, respectively) did not vary from expected (G's ≤ 3.67, df = 1, $P > 0.10$).

The number of stations in which at least one solicited contact of a Wood Thrush was recorded during the post-equilibrium period also differed from expected among the three trials in 1992 and 1993 combined ($G = 7.51$, df = 2, $P < 0.05$) (Fig. 1). The number of stations where one or more Wood Thrushes were noted did not differ from expected in both trials I (N = 77 of total, 30.1%) and II (N = 71, 27.7%) (G's ≤ 3.04, df = 1, $P > 0.10$). In contrast, the number of stations with solicited calls was lower than expected in trial III (N = 48, 18.8%) ($G = 7.27$, df = 1, $P < 0.01$).

Discussion.—Based on the results of our study, we believe that taped-playback songs are most useful as a means of soliciting Wood Thrushes early in the breeding season (e.g., trial I). A decline in response by Wood Thrushes to taped-playback songs later in the breeding season (e.g., only 41% of the total contacts in trial III were solicited vs. 63% in trial I) may be attributed to the nesting chronology. Although Wood Thrushes occasionally produce more than one brood (Harrison 1975), some pairs probably terminated breeding by mid- to late July, resulting in fewer solicited contacts than earlier in the breeding season.

Because unsolicited contacts comprised a lower percentage of the total contacts in trial I (37%) compared to either trial II (52%) or trial III (59%), we suspect that taped-playback songs helped elicit contacts of birds that otherwise would not sing or sang infrequently early in the breeding season (early June) without the use of taped-playback songs. Hence, use of taped-playback songs would increase the likelihood of detecting more Wood Thrushes than would otherwise be detected without the use of this technique. Furthermore, because singing

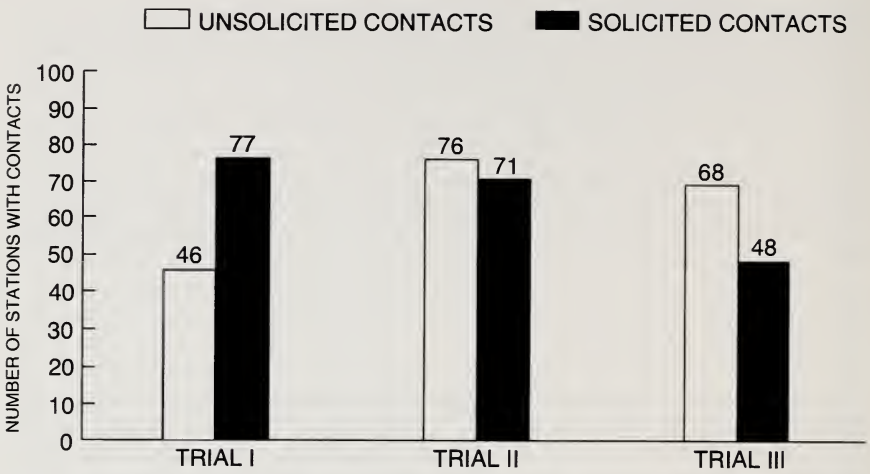

FIG. 1. The number of survey stations (N = 128) with unsolicited (1-min equilibrium period) contacts and solicited (4-min post-broadcast period) contacts of Wood Thrushes in early to mid-June, mid- to late June, and early to mid-July (trials I–III, respectively) during 1992 and 1993 combined at the Barrens Grouse Habitat Management Area, Centre County, Pennsylvania.

by Wood Thrushes tends to decline rapidly after sunrise (Robbins 1981), many of these birds probably would not be detected by an observer later in the morning without the use of taped-playback songs. We must caution, however, that there is a possibility that some birds responding to taped-playback songs were nonbreeding floaters in the population rather than breeding individuals.

In conclusion, we found that the use of taped-playback songs make transect surveys of breeding Wood Thrushes, as well as searches for active nests of thrushes (Yahner and Ross, unpubl. data), more efficient (labor or time), especially on relatively large study areas. An efficient protocol for surveying Wood Thrushes is important because breeding populations of Wood Thrushes have been given considerable attention in recent years (Hoover 1992, Roth and Johnson 1993, Bollinger and Linder 1994), in part because of regional declines in population numbers (Robbins et al. 1989, Askins et al. 1990, Robinson 1992). When surveying Wood Thrush populations, we recommend that taped-playback songs be used earlier (e.g., June) rather than later in the breeding season (e.g., July).

Acknowledgments.—We thank J. R. Gillis, S. P. Joyce, J. A. Sheesley, and J. S. Shuman for field assistance. This study was funded by the Pennsylvania Agricultural Experiment Station and the Max McGraw Wildlife Foundation.

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Wilson Bull., 107(4), 1995, pp. 742–746

Effects of laying date, clutch size, and communal nest size on the reproductive success of Monk Parakeets.—Monk Parakeets (*Myiopsitta monachus*) build conspicuous, enclosed stick nests, which are often large and which have several isolated chambers (Forshaw 1978, Martella and Bucher 1993). These chambers are occupied throughout the year by breeding pairs and non-breeding individuals (Martín 1989, Martella and Bucher 1993). The Monk Parakeet is iteroparous, monogamous, and breeds in the spring and summer (October to February) (Navarro et al. 1992). Although all members of a compound nest participate in the building, maintenance, and vigilance of the nest, only the breeding pair cares for the nestlings (Martella 1985, Martella and Bucher 1993). Few cases of allofeeding by members of different nests have been observed, which could function for the development of a communal breeding system (Martella 1985, Bucher et al. 1991).

Monk Parakeets have a variable clutch size (Navarro et al. 1992), the adaptive nature of which has been the subject of extensive discussion (e.g., Lack 1954, Perrins and Jones 1974). However, except for the research of Beissinger and Waltman (1991) on the Green-rumped Parrotlet (*Forpus passerinus*), this topic has been little studied in parrots.

In this paper we examine how laying date, clutch size, and the size of communal nest affect the reproductive success of Monk Parakeets.

Study areas and methods.—This study was carried out in 1982 near the town of Arroyito (31°25′S, 62°59′W) and from 1983 to 1988 close to the city of Jesús María (31°05′S, 64°11′W), in Córdoba Province, Argentina. Overall, we recorded 205 breeding attempts. Nest chambers were checked at seven to 12-day intervals from October to early March. This interval was selected to avoid a reduction of the breeding success due to observers disturbance (Navarro et al. 1992). In Arroyito, sampled nests were all grouped in *Eucalyptus* trees planted at both sides of the 1000-m long entrance to the ranch. In J. María, all nests were in the 610-ha study area in native trees. We could not sample very large nests (with more than ten individuals) because they were on inaccessible structures on powerline towers, windmills and tall trees. However, large nests comprised only 2% of the nests in both areas (Bucher et al. 1991).

Eggs found in each nest chamber were marked individually with indelible ink. Nestlings were identified by clipping different toenails and later were banded with numbered aluminum rings. The fate of each egg was recorded as either lost before hatching, failed to hatch, or hatched. Eggs that might have hatched but whose chicks disappeared before the following visit were assumed not to have hatched. Nestlings that disappeared from the nest before reaching fledging age (35 days; Navarro and Bucher 1990) were recorded as deaths. In doubtful cases, the survival was checked through capture-release procedures carried out three times a year during all the study (Navarro 1989; Martín and Bucher 1993). Initiation dates for clutches were determined by back-dating each clutch based on a 2.1-day interval between successive eggs, a 24-day incubation period (Navarro 1989), and the calculated age of nestlings (Navarro and Bucher 1990). Twenty-two clutches in which we could not estimate the onset of laying were discarded. To compare dates among years, we used the distance in days of a given date from the median date of first clutch for the population in that year, assigning negative values to those dates earlier than the median. First clutches refer to the first group of eggs laid in a given nest chamber in that season, replacement clutches are those started after failure of the first clutch, and second clutches are those laid after a successful first brood.

Results.—The earliest clutch was laid on 1 October 1983 and the latest on 29 October 1985. At both areas, 90% of first clutches within the population were laid within a nine week period (see also Navarro et al. 1992; Navarro and Bucher 1992). Clutch sizes ranged

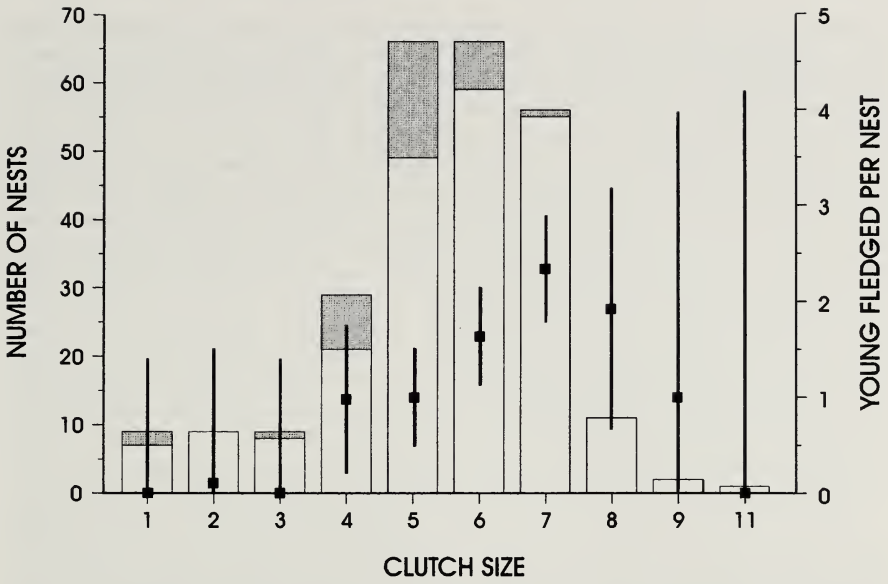

FIG. 1. Clutch size frequency (bars) and fledging success (squares) in Monk Parakeets. Open bars represent first clutches; shaded bars are replacement and second clutches. Vertical lines indicate 95% Tukey's HSD intervals above and below mean values.

from one to 11 eggs (mode = 6 eggs in first clutches); whereas replacement and second clutches ranged from one to seven eggs (mode = 5 eggs) (Fig. 1). First-clutches were significantly larger than second and replacement clutches (Mann-Whitney test; $Z = 3.27$; $P = 0.001$).

Clutch size decreased with the date of laying. As the breeding season advanced, first clutches were smaller (Spearman Rank Correlation; $r_s = -0.290$, N = 200, $P < 0.001$).

Hatching success was significantly correlated to laying date and clutch size. Hatching success decreased throughout the nesting season when a partial correlation was used to hold clutch size constant (Partial Correlation coefficient; $R_p = -0.225$, N = 200, $P < 0.01$), and, in turn, increased with the clutch size when laying date was held constant ($R_p = 0.332$, N = 200, $P < 0.01$).

Fledging success was not correlated with either laying date ($R_p = -0.050$, N = 200, $P > 0.05$) or clutch size ($R_p = 0.123$, N = 200, $P > 0.05$) when clutch size and relative laying date were held constant, respectively.

As a result of both the greater number of eggs and the higher hatching success of larger clutches, the number of young fledging per pair increased with clutch size. The most productive clutches were those of seven eggs, but they did not differ significantly from clutches of six or ≥ eight eggs (Fig. 1). Virtually none of the clutches of one to three eggs successfully fledged young (Fig. 1). The low frequency of these small clutches led us to think that they could be the result of undetected layings and subsequent predation (between visits), or due to the desertion or death of at least one member of the pairbond. Furthermore, their low productivity is likely to be a consequence of any of these factors.

Laying date of first clutches did not affect wether females laid a replacement or second clutch. Early and late breeders did not differ in the frequency of starting replacement or

second clutches ($\chi^2 = 0.155$, df = 1, $P = 0.7$). Nevertheless, the date of the onset of laying had a significant effect on the chances of producing at least one young from the first clutch. Early breeding pairs (those that began their first clutch before the respective median date of each year) produced at least one young in 55% of the first clutches started compared to only 39% for late breeders ($\chi^2 = 4.79$, df = 1, $P = 0.029$).

Laying date of first clutches was significantly negatively correlated with the number of parakeets inhabiting compound nests ($r_s = -0.256$, N = 184, $P < 0.001$). First clutches were laid earlier in larger nests. Hatching success and fledging success of first clutches had positive but non-significant relationships with the number of individuals occupying the compound nest, when the date of onset of laying was held constant by partial correlation ($R_p = 0.140$ and $R_p = 0.083$, N = 184; respectively).

The productivity of a nest chamber depended on the date of laying but not on the number of individuals inhabiting the compound nest to which it belongs. The total number of young fledged from a nest chamber throughout the season (considering all clutches that had been laid) was significantly correlated with the laying date of first clutch when the number of individuals in the compound nest was held constant ($R_p = -0.262$, N = 184, $P < 0.01$). On the other hand, when date was held constant, the number of young produced was not correlated with the number of individuals inhabiting the nest ($R_p = 0.075$, N = 184).

Overall, the total number of young fledged from breeding chambers in compound nests that were occupied by more than four birds (median value) was higher (but not significantly) than fledging success of smaller nests ($Z = 0.693$; N = 43 and 162, respectively; $P = 0.488$). Also, the proportion of successful breeding pairs (first clutches only) in nests inhabited by more than four birds (55.8%) was higher (but not significantly) than that of smaller nests (42.6%) ($\chi^2 = 2.397$; df = 1; $P = 0.122$). This difference was even lower when first and non-first clutches were considered together.

Discussion.—Our results show that the date of laying was the most important correlate of reproductive success in Monk Parakeets. Laying date correlates both with the clutch size and hatching success, so on average early clutches are larger and produce more nestlings and, consequently, more fledglings than late clutches (because the fledging success is independent of date and clutch size). This result coincides with the observations of Beissinger and Waltman (1991) in Green-rumped Parrotlet, in which the number of young increased with clutch size. In addition, in the Monk Parakeet early clutches are more likely to produce at least one juvenile than late clutches.

There is a slight trend by breeding pairs inhabiting large nests to start egg laying earlier in the season. In larger nests, interactions among individuals such as social stimulation, self-maintenance behavior (e.g., foraging) and nest construction and maintenance, are facilitated (e.g., all members of a compound nest participate in bringing material to the nest and in building and maintenance activities) (Bucher et al. 1991, Martella and Bucher 1993). These interactions seem to play an important role in the Monk Parakeet breeding system (Martella 1985, Bucher et al. 1991), and could promote earlier laying attempts.

Despite the above mentioned trend, individuals inhabiting larger nests do not have, on average, a significantly higher productivity nor chances of being successful with their first clutch compared to individuals at smaller nests. Larger nests are frequently occupied simultaneously (in different chambers) by adults with breeding experience and inexperienced breeders (two-year-olds; Martella 1985, Martín and Bucher 1993). Taking into account that either experienced or novice breeders are physiologically capable of breeding, and that egg laying could be not as costly to females as rearing the young, as proposed by Waltman and Beissinger (1992) in Green-rumped Parrotlet, one can expect that all pairs should begin a clutch. However, unskilled breeders could not always be "ready" (see below) for facing the

effort of taking care of a large brood. Therefore, the lower success of inexperienced breeders could be contributing to reduce the average productivity of large communal nests.

Given that the Monk Parakeet is a long lived species (about 5 years on average and 12 years maximum; Martín 1989), the reduction of its reproductive output could be explained by the "restraint" hypothesis, the "constraint" hypothesis, or a combination of both (Curio 1983). If additional breeding effort required to rear a large brood under unfavorable conditions could reduce the individual's probability of subsequent survival, young Monk Parakeets should refrain from investing maximally in actual reproduction and should increase their breeding effort as they become older to maximize lifetime reproductive success. Besides, the less successful breeding attempts may allow Monk Parakeets to gain experience and, therefore, to improve their breeding performance in following breeding seasons.

Lack's (1954) suggested that the most common clutch size should be the most productive. However, the Monk Parakeet's modal clutch size (six eggs) was not more productive than larger clutch sizes. This argues against Lack's prediction, but agrees with other studies in parrots (Smith and Saunders 1986, Beissinger and Waltman 1991) and other bird species in which deviations from Lack's principle have been ascribed either to differences in female age, experience and condition, or to territory quality (e.g., Klomp 1970, Winkler and Walters 1983). Under the assumption that reproductive restraint or constraint hypotheses are operating, one could expect that the frequency distribution of clutch sizes of Monk Parakeets would not fit to Lack's (1954) predictions.

All above mentioned issues are closely related and, as consequence, this study is not conclusive about the forces driving the reproductive success in the Monk Parakeet. Although under field conditions it could be difficult to tease apart their effect, further research focused on these topics is required.

Acknowledgments.—We thank A. Gómez Durán and the Romanutti family for the use of their properties as study areas, and the Campos family for their kind hospitality throughout the study. The Cooperativa Eléctrica of Arroyito provided logistical support. L. Martín, H. Merlini, P. Wallace, and S. Miglietta gave us helpful aid during fieldwork. M. Nores made valuable comments on an earlier draft of this paper. We are also indebted to S. R. Beissinger and an anonymous referee for critically reading the manuscript. The Consejo Nacional de Investigaciones Científicas y Técnicas of Argentina (CONICET) provided funds through post-graduate scholarships to J.L.N. and a research grant to E.H.B. (PID 3-908101/85).

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Wilson Bull., 107(4), 1995, pp. 746–752

The influence of Yellow-bellied Sapsuckers on local insect community structure.— Natural communities consist of irregular patchworks of organisms whose relative abundances both reflect and influence environmental heterogeneity (e.g., Diamond and Case 1986, Cornell and Lawton 1992). Within a given habitat, any species that augments environmental patchiness is likely to influence the abundances of sympatric species. For instance, through their unusual foraging strategy, Yellow-bellied Sapsuckers (*Sphyrapicus varius*) create rich resource patches in the form of sapwells, and may thereby affect population densities and spatial distributions of many co-occurring species.

The Yellow-bellied Sapsucker feeds primarily on phloem and sap obtained through the excavation of sapwells. A sapwell consists of horizontal rows of shallow holes drilled into bark, into which sap flows (Tate 1973). Sapsuckers drill newer rows directly above older wells, producing a two dimensional array of shallow holes. While the volume and quality of sap flow depend on both the tree species and the daily rates of transpiration and photosynthesis (Foster and Tate 1966), flow can often be considerable and sap often contains 20–30% sucrose (Tate 1973). Insects comprising seven orders and 20 families have been found associated with sapwells (Foster and Tate 1966). Preferential orientation of insects toward rich resource patches may be manifest as increased abundance and/or diversity of nectivorous insect communities in close proximity to sapwells. Therefore, by serving as a focal point for insect aggregation, sapwells may influence the local community structure (i.e., absolute and relative abundances) of the nectivorous insect guild. The purpose of this study was to determine (1) whether sapsucker foraging influences local insect diversity and species

richness and, if so, (2) which insect taxa are most strongly influenced by the presence of sapwells.

Study area and methods.—To determine whether the presence of sapwells influences the local insect community, insect visitation was monitored at 16 artificial sapwells located at the University of Michigan Biological Station (UMBS) in Cheboygan County, Michigan. Artificial sapwells were established in paper birch trees (*Betula papyrifera*) by using a 4.8 mm-($^3/_{16}$ inch) diameter steel punch to create an array of holes resembling an active sapwell. In addition, adjacent bark was roughened with sandpaper to simulate recent sapsucker attendance. A 1-liter plastic bottle containing 30% sucrose solution (intended to mimic natural birch sap; Tate 1973) was mounted 25 cm above each artificial sapwell. Surgical tubing was run from the mouth of the bottle to the sapwell and drip rate was manipulated to simulate natural sap flow.

Eight sets of sapwells were established, each located in a separate sapsucker territory. Each set consisted of one active natural sapwell, and a pair of artificial sapwells (sampling stations), one located on a birch tree approximately 5 m from the natural sapwell and a second located on a birch tree approximately 40 m from the same natural sapwell. The near artificial sapwell sampled the insect community in close proximity to a natural sapwell, while the far artificial sapwell sampled the insect community far from a natural sapwell. Paired artificial sapwells were located in similar microhabitats and microclimates resembling those of the natural sapwells.

Each artificial sapwell was observed for one 20-min interval on each of 11 days between 25 July and 7 August 1992. Pairs of artificial sapwells were visited in random sequence. During each sample period, the number and identity of all insects visiting each artificial sapwell was recorded. Care was taken to avoid counting any individual more than once. When necessary, representative specimens were collected for subsequent identification. The majority of specimens was identified to family, and in all cases specimens were identified to the lowest possible taxonomic category permitted by the authors' expertise.

To determine whether artificial sapwells accurately mimicked natural sapsucker sapwells, insect visitation was also observed at two additional active natural sapwells in separate territories. Observational methods at natural sapwells were identical to those at artificial sapwells except that natural sapwells were visited on only three days.

To determine whether sapsuckers influence local insect community structure, total insect visits were compared between the near and far artificial sapwells of each pair, using paired *t*-tests. For the entire assemblage of insects visiting each artificial sapwell, we calculated four measures (1) a Shannon-Weiner diversity index (H′), appropriate because a small subset of the entire insect community was sampled; (2) evenness or relative diversity (J′), calculated as the ratio of the observed diversity to the maximum possible, given the same number of species; (3) species richness, defined as the total number of species observed; and (4) total number of individuals observed. In addition, we used Chi-square analysis to determine whether the relative abundances of insect species differed between areas near to vs far from a natural sapsucker sapwell. Where necessary, species containing few individuals were lumped into higher taxa, e.g., family or order.

Results.—A total of 2227 insects was observed during this study (1351 at artificial sapwells near to a natural sapwell and 876 at artificial sapwells far from a natural sapwell). The total number of visiting insects was significantly higher at artificial sapwells located near to a natural sapwell ($P = 0.035$; Table 1). Similarly, species richness was significantly higher and evenness was nearly significantly higher at near than at far artificial sapwells ($P = 0.002$ and $P = 0.083$, respectively; Table 1). In contrast, species diversity did not differ significantly between near and far artificial sapwells ($P = 0.18$; Table 1).

Differences in community composition were also evident from inspection of individual

TABLE 1

CHARACTERISTICS OF INSECT COMMUNITIES NEAR TO AND FAR FROM NATURAL SAPWELLS[a]

Characteristic	Near sapwells	Far sapwells	Paired *t*-statistic	*P*-value
Total number of individuals	168.9 (60.8)	109.5 (27.2)	2.61	0.035
Species richness	11.8 (1.9)	6.4 (4.4)	4.68	0.002
Diversity (H′)	0.45 (0.15)	0.39 (0.13)	1.49	0.180
Evenness (J′)	0.43 (0.09)	0.29 (0.10)	2.02	0.083

[a] Means are given with standard deviations in parentheses. Sample size was eight for each sapwell location.

species and species groups. Relative abundances of insect species differed significantly between near and far artificial sapwells ($P < 0.0005$; Table 2). Coleoptera, Diptera (exclusive of the Tephritidae), bald-faced hornets, and particularly Lepidoptera were more abundant than expected near to a natural sapsucker sapwell. In contrast, Collembola, Psocoptera, and ants were less abundant than expected near to a natural sapsucker sapwell (Table 2). In

TABLE 2

TOTAL NUMBER OF INDIVIDUALS FOR COMMON INSECT TAXA AT NEAR AND FAR SAPWELLS[a]

Taxon	Total number of individuals		Partial χ^2
	Near sapwells	Far sapwells	
Lepidoptera			
Tortricidae	16	0	10.39
Mourning Cloaks (*Nymphalis antiopa*)	10	0	6.39
Misc. Lepidoptera	14	3	3.37
Hymenoptera			
Yellow jackets (*Vespula* spp.)	854	574	0.44
Bald-faced hornets (*Dolichovespula* spp.)	63	27	3.28
Formicidae	313	229	1.94
Misc. Hymenoptera	11	7	0.00
Diptera			
Tephritidae	11	6	0.12
Misc. Diptera	26	6	5.70
Coleoptera	17	3	5.02
Psocoptera	11	12	1.64
Collembola	5	9	3.67
Total	1351	876	41.96

[a] Relative abundances differed significantly among sapwell locations ($\chi^2 = 41.96$, df = 11, $P < 0.0005$).

addition, one order and 20 families were observed near to but not far from natural sapwells; of these, seven families were observed also at natural sapwells. Six families were observed far from but not near to natural sapwells; however, of these, only one family was observed at natural sapwells (Table 3).

Discussion.—The results of this study suggest that the presence of Yellow-Bellied Sapsuckers can strongly influence local insect community structure. We observed significantly higher numbers of individuals and species richness, and nearly significantly higher species evenness, at artificial sapwells near to natural sapsucker sapwells compared to similar artificial sapwells that were far from natural sapsucker sapwells. Moreover, these differences were observed despite a generally conservative experimental design; for instance, the significantly higher total number of insects at near vs far artificial sapwells arose in spite of potential competition between natural sapwells and near (but not far) artificial sapwells.

Sapsucker sapwells represent a rich resource patch that is exploited by a wide variety of insect species, families and orders. We observed 14 families associated with natural sapwells; to our knowledge only 11 families have previously been reported (Bolles 1891; Nickell 1956, 1965; Foster and Tate 1966). Most observed taxa are nectivorous, with the exception of Collembola, which are generally associated with fungi and decaying wood. Of particular interest, sap beetles (Coleoptera: Nitidulidae) were observed only at natural sapsucker sapwells and at nearby artificial sapwells. Sap beetles feed exclusively on decaying fruit and fermenting plant juices, which appear to be scarce resources in most temperate forest habitats. This family may therefore depend on sapsuckers to augment an environment otherwise impoverished in such resources.

Foraging behavior varies considerably among the taxa of insects observed exploiting our artificial sapwells. The considerably higher relative abundance of Hymenoptera (particularly vespid wasps and ants) at near vs far sapwells (63% vs 23%) may indicate the importance of learning in this group. Artificial sapwells in close proximity to natural sapsucker sapwells may have been more rapidly discovered and therefore more often visited during this study. Presumably, learning-based site fidelity by these Hymenoptera was more influential than their ability to disperse over reasonable distances. Similarly, Lepidoptera are capable of learning information that allows increased foraging efficiency (Lewis 1988) and, despite their well-developed dispersal capacity, also displayed greater relative abundances at near vs far sapwells (2.96% vs 0.003%; Table 2).

Many patch-foraging insect species exploit a single patch until the resource is nearly exhausted (Heinrich 1979). A sapsucker sapwell is a rich and generally scarce resource patch. The spatial distribution of sapwells in northern forest habitats may therefore favor short-term, intensive patch exploitation (Real 1991).

Our results suggest that natural Yellow-bellied Sapsucker sapwells are a rich resource patch actively exploited by a wide variety of insect species. Similarly, Ehrlich and Daily (1988) and Daily et al. (1993) have shown that sapwells of the Red-naped Sapsucker, *Sphyrapicus nuchalis,* provide nourishment to over 40 insect species within subalpine Rocky Mountain ecosystems. Together, these observations indicate that, across a variety of habitats, the presence of sapsuckers may strongly influence the size, composition, and spatial distribution of local insect communities, just as they can influence the structure of local bird communities (Miller and Nero 1983, Daily et al. 1993).

Acknowledgments.—We thank the National Science Foundation Research Experience for Undergraduates Program for supporting this research, and the Univ. of Michigan Biological Station for providing logistic support. We also thank Ted Anderson for helpful advice on experimental design and Laurie Eberhardt for assistance in locating sapsucker territories.

TABLE 3

INSECT TAXA IDENTIFIED DURING AT LEAST ONE SAMPLING PERIOD FROM NATURAL, NEAR AND FAR SAPWELLS

Family/species	Sapwell location		
	Near	Far	Natural
Lepidoptera			
Argyresthiidae	×		
Geometridae	×		
Itame pastularia		×	
Noctuidae	×	×	
Catacala ilia			×
Nymphalidae	×		
Limenitis arthemis astyanax			×
Nymphalis antiopa			×
Nymphalis vau-album			×
Lethe anthedon		×	
Tortricidae	×		
Satyridae			×
Microlepidoptera	×	×	
Hymenoptera			
Apidae		×	
Braconidae	×		
Chrysididae	×		×
Formicidae	×	×	×
Ichneumonidae		×	
Pompilidae	×	×	
Sphecidae	×	×	
Tiphiidae	×		
Tiphiinae sp.		×	
Vespidae			
Vespula sp.	×	×	×
Diptera			
Calliphoridae	×		×
Dolichopodidae	×		×
Drosophilidae			×
Lauxaniidae		×	
Heleomyzidae	×		
Milichiidae			×
Muscidae (2 spp.)	×		×
Psocidae		×	
Sciuridae	×		
Tachinidae	×		
Tephritidae	×	×	×

TABLE 3
CONTINUED

Family/species	Sapwell location		Natural
	Near	Far	
Coleoptera			
Cantharidae	×		
Carabidae			
Calosoma sp.	×		
Curculionidae	×		×
Dermestidae			
Trogoderma sp.			×
Elateridae		×	
Nitidulidae (3 spp.)	×		×
Scarabacidae			
Osmoderma sp.	×		
Scolytidae		×	
Silphidae			
Silpha sp.	×		
Hemiptera			
Pentatomidae		×	
Homoptera			
Membracidae	×		
Collembola			
Eutomobryidae	×	×	
Psocoptera			
Psocidae	×	×	

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Wilson Bull., 107(4), 1995, pp. 752–756

Diurnal activity budgets of pre-nesting Sandhill Cranes in arctic Canada.—Lack (1968) contended that waterfowl clutch size evolved in relation to female food consumption during egg formation. Ryder (1970) modified this hypothesis noting that several arctic-breeding geese did not feed during egg-laying. Those geese probably used nutrients accumulated on wintering and staging areas to lay and incubate clutches (Ankney and MacInnes 1978, Raveling 1979). More recent studies of endogenous reserves and the amount of time spent feeding when at, or near to, the ultimate breeding areas before clutch initiation have suggested that this simple model does not apply to all populations (e.g., Greater White-fronted Geese [*Anser albifrons*], Fox and Madsen 1981, Budeau et al. 1991; Canada Geese [*Branta canadensis*], Bromley and Jarvis 1993), even geese breeding in the high arctic (e.g., Snow Geese [*Anser caerulescens*], Gauthier and Tardif 1991).

Sandhill Cranes (*Grus canadensis*) allocate less nutrients to clutch formation in relation to body size than northern nesting geese (ca 7% vs 17%, Bromley, unpubl. data), and generally are believed to acquire necessary nutrients for migration and reproduction at spring staging areas (Krapu et al. 1985). This enables arriving cranes to cope with highly variable weather conditions encountered on arctic breeding areas and initiate clutches with minimal local exogenous supplement to their nutrient reserves.

Both Sandhill Crane sexes share incubation. As female cranes contribute comparatively less nutrient investment to the clutch and to incubation than geese, we hypothesise that there is less male investment in vigilance and female protection, more time spent in maintenance or improvement of condition by the male and less time feeding by females than in arctic nesting geese. During a study of pre-nesting waterfowl in the central Canadian Arctic, we tested the predictions that: (1) male cranes feed less and spend more time alert than females, but that the differences would be less marked than among arctic nesting geese, and (2) the nesting phenology of cranes precede that of locally breeding Greater White-fronted and Canada geese because: (1) most of the cranes' reproductive material is endogenously de-

rived, and (2) first egg-date of cranes is more dependent on snow melt (i.e., nest site availability) than on female acquisition of nutrient reserves.

Study area and methods.—Pre-nesting behavioral observations were made in 8 km² of tundra at the Walker Bay Field Station (WBFS) of the Northwest Territories Department of Renewable Resources on the Kent Peninsula, NWT, Canada (68°20′N, 108°05′W). This area has been used for the long-term study of Canada and Greater White-fronted geese since 1990, and goose observations from other seasons are presented here where appropriate. We sampled paired Sandhill Crane activity from 28 May to 5 June 1992 by scan sampling a segment of 110° from WBFS, scoring each individual according to its sex (males distinguished by their larger size and longer bills than females, Tacha et al. 1992), locomotory status (sit, stand, walk, run, fly) and activity/posture (alert, head low, sleep, feed, social activity, sexual behavior, comfort activity etc). In the analysis, these categories were combined as far as possible to be comparable with the behaviors described by Tacha et al. (1987), namely searching, feeding, locomotion, resting, comfort and social. We distinguished "alert" behavior, recorded when a bird was standing with its head up, from "social" as defined by Tacha et al. (1987). Scans were carried out every 15 min, scoring male and female activity separately from between four and 12 pairs present in the study area, recording 144 scans evenly spread throughout the 24-h period. The data base comprised 1723 individual observations up until the discovery of the first egg on 5 June.

Snow cover on the study area declined from 98% on 24 May to 75% by 5 June (based on regularly walked transects); snow melt was the latest during 1992 of the five studied seasons 1990–1994 inclusive, mainly as a result of prolonged sub-zero temperatures during 29 May–2 June inclusive. Sandhill Cranes were not much in evidence in the study area during 24–27 May, with only single pairs observed intermittently. From 28 May, four pairs were regularly present in the study area and observations commenced at 14:00 h that day. Date of clutch initiation was determined by direct observation. Greater White-fronted and Canada geese nests were found by active search, direct observation and flushing females in the course of other activities. First egg dates for cranes and geese were established on the basis of an average laying interval of 33 h.

Results.—Cranes were paired on arrival; no larger groups were seen until after nest initiation. There were few territorial clashes, pairs were consistent in their use of the study area, foraging in snow-free patches close to their ultimate nest sites. The overall activity budget, summarized by two-h periods (Fig. 1) indicated cranes fed for 33.5% of the 24-h daylight period, rested (slept) for 37.8%, spent 15.4% of the time in locomotion and were alert 13.0% of the time. Courtship, comfort and other minor activities combined comprised less than 1% of the remainder. Resting behavior was inversely correlated with alertness ($r = -0.694$, $P < 0.05$), locomotion ($r = -0.919$, $P < 0.01$), feeding ($r = -0.795$, $P < 0.01$) and searching ($r = -0.635$, $P < 0.05$); alert behavior was positively correlated with locomotion ($r = 0.551$, $P < 0.05$) and feeding ($r = 0.552$, $P < 0.05$); locomotion was positively correlated with feeding ($r = 0.645$, $P < 0.05$) and searching ($r = 0.670$, $P < 0.05$). Hence, cranes showed marked changes between the active and resting phases of their daily behavior.

Male cranes spent more time alert (16.3% vs 9.6%, *t*-test, $P < 0.001$) and fed less (26.8% vs 40.2%, *t*-test, $P < 0.001$) than females. Male and female time budgets were not significantly different for all other major activities (locomotion 14.5% vs 12.6%, rest 39.8% vs 35.8, search 2.1% vs 1.4%, other activities 0.5% vs 2.4%, *t*-tests, $P > 0.05$ for all activities). Male cranes spent proportionally less time alert and more time feeding than females compared with studied goose species, while female cranes were more alert and fed less than female geese (Table 1). Nesting was highly synchronous in all species (Table 2). Although Crane nesting densities were extremely low in this tundra habitat, all seven nests were initiated between 5 and 10 June ($\bar{x}$ = 6 June). Most Canada Goose clutches were initiated

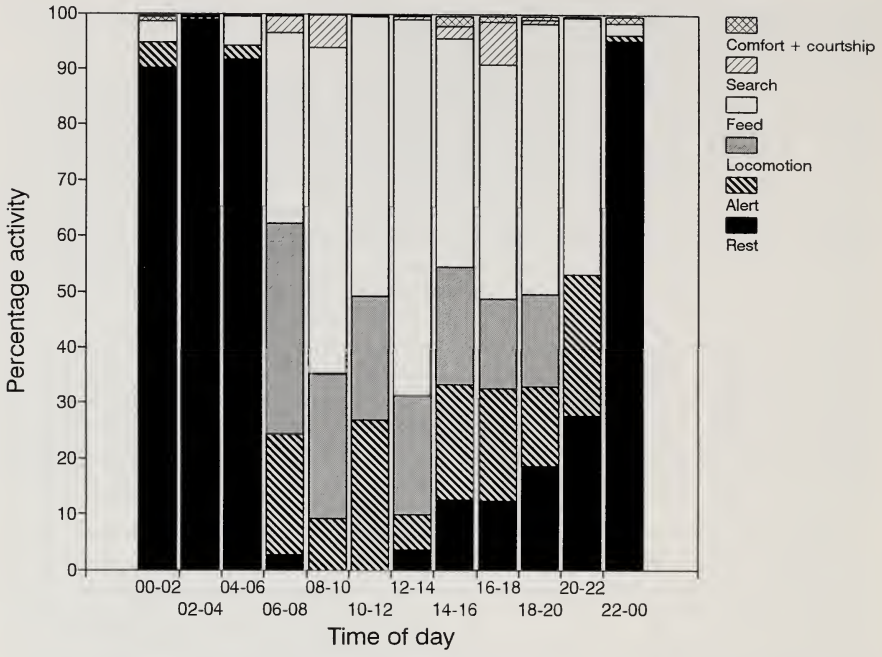

FIG. 1. Diurnal patterns of activity of Sandhill Cranes from Walker Bay Field Station, Northwest Territories, spring 1992.

TABLE 1

COMPARISON OF THE RATIO BETWEEN FEEDING AND ALERT BIRD BUDGETS[a] FROM PUBLISHED ACCOUNTS OF PRE-NESTING FEEDING IN ARCTIC-NESTING GEESE WITH DATA FOR SANDHILL CRANES FROM WALKER BAY FIELD STATION, NWT

Study	Species	Alert ratio of female to male allocation	Feeding ratio of female to male allocation
Budeau et al. (1991)	Greater White-fronted Goose	0.15	1.98
Fox and Madsen (1981)	Greater White-fronted Goose	0.23	1.91
Gauthier and Tardif (1991)	Snow Goose	0.20	1.72
This study	Crane	0.59	1.50
This study[b]	Greater White-fronted Goose	0.15	1.53
This study[b]	Canada Goose	0.12	1.60
Mean values WBFS 1990–1993[b]	Greater White-fronted Goose	0.19	1.59
Mean values WBFS 1990–1993[b]	Canada Goose	0.15	1.72

[a] Values indicate the ratio of the percentage of time spent by females to that spent by males from each of the studies.
[b] Unpubl. data.

TABLE 2

FREQUENCY DISTRIBUTIONS OF FIRST EGG DATES OF GREATER WHITE-FRONTED GEESE, CANADA GEESE, AND SANDHILL CRANES FROM WALKER BAY FIELD STATION, SPRING 1992

Date	Greater White-fronted Goose	Canada Goose	Crane
5–6 June	0	0	4
7–8 June	0	0	3
9–10 June	3	3	0
11–12 June	3	7	0
13–14 June	1	10	0
15–16 June	8	1	0
17–18 June	2	2	0

on 13 June and eight out of the 17 Greater White-fronted Goose clutches were initiated during 15–16 June.

Discussion.—At WBFS, time devoted to feeding by pre-nesting female Cranes (40%) was less than geese during the same year (59% in Greater White-fronted Geese in 1992, range 55–65% from four seasons 1990–1993 and 66% in Canada Geese, range 57–73% for three seasons 1991–1993 Bromley, unpubl. data), and from other studies (e.g., 68% in Greenland White-fronted Geese [*A. a. flavirostris*], Fox and Madsen 1981, 76% in Snow Geese, Gauthier and Tardif 1991). Early arriving cranes probed for below-ground plant storage organs as well as lemmings (abundant during early spring 1992), and scavenged caribou (*Rangifer tarandus*) carcasses. Such food items offered a more profitable feeding resource per unit dry weight, but require more search and handling time than the intensive grazing and probing which formed the basis for goose foraging.

Female cranes fed more than males before nesting, an observation which fits the model of pair-bond investment in long-lived monogamous birds such as the geese and cranes, in which a female maximizes energy intake in preparation for reproduction, while the attendant male sacrifices feeding time to protect her from other males and potential predators. The major differences between crane and goose behavior were the reduced male crane investment in vigilance, plus the smaller proportion of time spent feeding and the larger proportion of time spent alert by the female. Since cranes share the burden of incubation (in contrast to geese), these observed patterns fit with the model of a trade-off between investment in female protection through male vigilance and a need to maximise reserves to improve fitness in the face of the incubation burden placed upon the male. The male benefits by spending proportionally more time feeding, enabling an increased role in incubation which in turn gives the female greater flexibility not to feed early after arrival to accumulate reserves to see her through incubation.

It is likely that the late 1992 season had a considerable impact upon the behavior and possibly on the timing of crane breeding at WBFS. However, in other years, there appeared little correlation between nest initiation dates and snow melt (unpubl. anecdotal information). The presence of persistent snow cover may have greatly influenced food availability for both cranes and their predators. There is a need for further study of Sandhill Crane feeding behavior prior to clutch initiation before we can be confident that this species relies to a greater extent on endogenous reserves accumulated on staging areas for reproduction than do the geese nesting in the same area. However, the results presented here support the assertion that Sandhill Cranes can commence laying eggs earlier than geese in an abnormally

late season. Our observations also support the hypothesis that male cranes spend proportionally less time alert and more time feeding than male arctic nesting geese, presumably as a consequence of the increased physiological demands of shared incubation. Mirroring the different reproductive strategies, female cranes feed less than geese during prelaying because their relative reproductive investment is lower, because male cranes share in incubation.

Acknowledgments.—We thank the Canadian Wildlife Service for support to H.B. and A.D.F. and the Northwest Territories Department of Renewable Resources for support to carry out the study. We thank Bruno Croft for his enormous logistical support and the many others who have supported the work of the WBFS program. The Polar Continental Shelf Project of Energy, Mines and Resources Canada provided transportation from the study area in June. Thanks to Myrfyn Owen for allowing the participation of A.D.F. in the project. Preben Clausen, Karsten Laursen, Carroll Littlefield and an anonymous referee all improved on an earlier manuscript.

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Wilson Bull., 107(4), 1995, pp. 757–761

Mate guarding tactics used by Great Crested Flycatchers.—To counter female infidelity, male birds have evolved several behaviors which increase their probability of paternity. Mate guarding may be defined as any behavior by a mated male whose principal function is to decrease the likelihood of his mate copulating with other males during the period when her eggs can be fertilized (Birkhead 1979, Beecher and Beecher 1979, Hatch 1987). Most studies of mate guarding focus on following behavior. Mate guarding is inferred from following behavior if males follow their mates more often when the females are fertile than when they are non-fertile (e.g., Gowaty and Plissner 1987). Territoriality may also function as mate guarding. By defending a larger breeding territory during his mate's fertile period, a male increases the distance between his mate and intruding males (Møller 1990; but see Dunn 1992).

We investigated mate guarding in the socially monogamous Great Crested Flycatcher (*Myiarchus critinus*). We predicted that males in this species would attempt to increase their probability of paternity by using one or both of these forms of mate guarding behavior. First, we compared the tendencies of males to follow their mates during vs after the female's fertile period; second, we measured territory size throughout the breeding season to determine whether males defend larger territories when paternity is at stake. Here we present evidence that male Great Crested Flycatchers do guard their mates.

Methods.—We studied six pairs of Great Crested Flycatchers breeding in natural cavities around the Queen's Univ. Biological Station, near Kingston, Ontario, from 16 May to 30 July 1991. We located all nests during nest-building, and monitored each pair until about six days after hatch, when brooding stopped. In this species, only females build the nest, incubate eggs and brood young (Taylor and Kershner 1991), so we could determine the sex of adults through behavioral observations at the nest site. During the breeding season, these birds aggressively defend territories (Bent 1942). Therefore, we were confident that birds seen tending the same nest on different days were the same individuals. As in other studies, we considered females to be fertile during nest-building and egg-laying (Birkhead and Møller 1992). We divided our observations of following and territory size into fertile and post-fertile categories.

We performed watches at each nest site, because it is difficult to track these birds through the forest. Each watch lasted one hour, and was performed between 06:00 and 18:00 h EST, alternating early morning and afternoon watches on subsequent days. During each watch, we recorded visits of the birds to the nest site. For each visit, we determined the sex of the birds, and then categorized the visit into one of three categories: male following, female following, or no following. If the birds visited the nest site, within 5 sec of one another, and flew in the same direction, we considered the second bird to be 'following'. Otherwise, the visit was scored as 'no following'. For each of the six pairs, we observed 16–226 visits in each of the fertile and post-fertile periods.

We measured territory size during playback trials (Falls 1969) to determine whether males defended larger territories during the female's fertile period. The recording used for playback consisted of a loop of Great Crested Flycatcher calls from a commercial recording. We began each playback trial when both birds were observed at the nest site. At this time we played back the recording at a consistent volume, from an initial distance of 10 m, and slowly walked away from the nest at a steady pace. The distance that the male ceased responding to the playback was measured as the response radius. We performed 1–4 playbacks in both the fertile and post-fertile periods to each of three pairs, over four breeding attempts (one pair nested twice). We then calculated the mean radius of response for each male in both the fertile and post-fertile periods. Males' response to repeated playback may

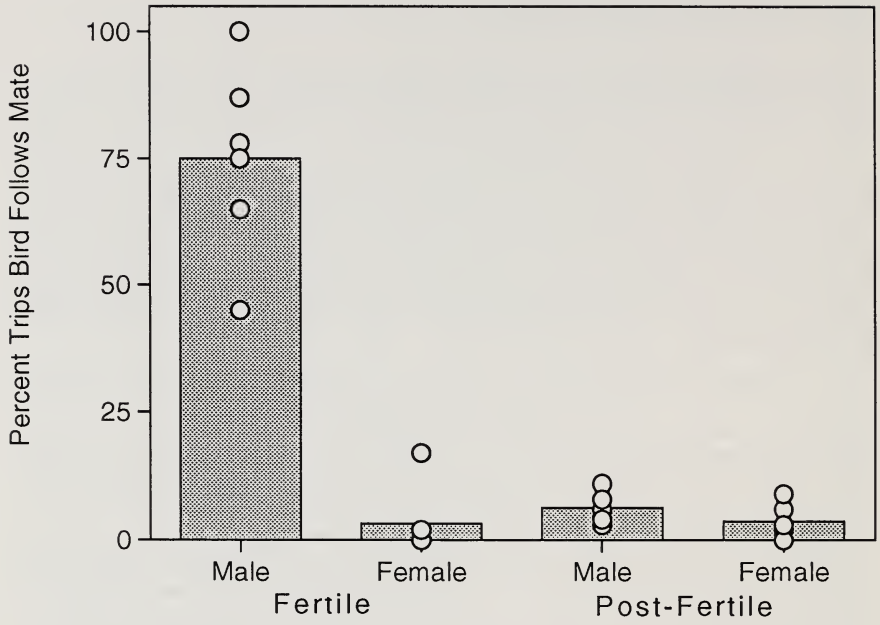

FIG. 1. Percentage of visits to the nest in which six male and six female Great Crested Flycatchers followed their mates, during the fertile and post-fertile periods. Open circles represent individual tendencies to follow a mate; bars indicate group means.

change independently of territory size due to learning, either decreasing (Verner and Milligan 1971) or increasing (Knight and Temple 1986). To reduce these effects, we performed playback trials at least four days apart.

Results.—Males were more likely to follow their mates during the fertile period than during the post-fertile period (Fig. 1). As well, males followed females more often than females followed males during the fertile period (Fig. 1). For each period (fertile and post-fertile), we calculated the proportion of visits that males followed females or females followed males. These proportions are independent because during a number of visits, neither bird followed. A two-way repeated measures ANOVA on the arcsine-transformed data revealed a main effect of sex ($F = 33.7$, df = 1,10, $P = 0.0002$), a main effect of period ($F = 30.2$, df = 1,10, $P = 0.0003$), and a significant interaction ($F = 30.0$, df = 1,10, $P = 0.0003$). That is, males followed females more during the fertile period than during the post-fertile period, or than females followed males at all.

Territory size tended to decrease from the fertile period to the post-fertile period. That is, the radius of response to playback decreased from the fertile to the post-fertile period in three of four nesting attempts (Fig. 2). Although the decrease in response radius was statistically significant (one-tailed paired *t*-test, $t = 2.42$, df = 3, $P = 0.047$), this analysis includes observations made on a pair which renested after their first nest failed. During the second nesting attempt, the territory dynamics matched the general trend observed; response radius increased during the second fertile period, and subsequently decreased. Exclusion of this second nesting attempt reduces our sample size to the point where inferential statistics are unwarranted.

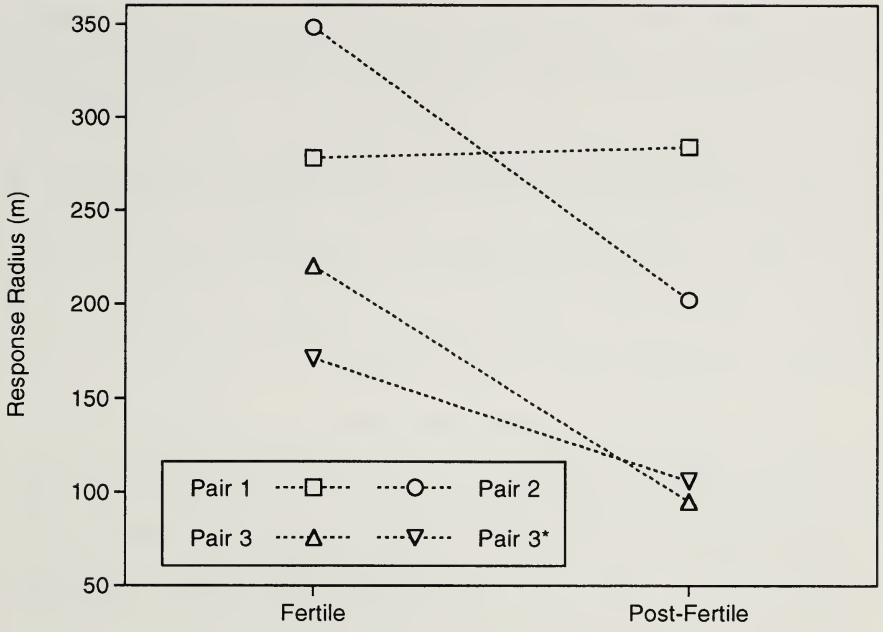

FIG. 2. Mean radius of response to playback (distance from the nest at which male Great Crested Flycatchers stopped responding to song playback), during the fertile and post-fertile periods. 'Pair 3*' refers to the second nesting attempt by pair 3.

Discussion.—The pattern of following by males, during their mates' fertile and post-fertile periods (Fig. 1), strongly suggests that male Great Crested Flycatchers use close surveillance to guard their mates. Several alternative hypotheses have been proposed for close male attendance during the fertile period (e.g., Power 1980, Lumpkin et al. 1982, Gowaty and Plissner 1987), but our results do not support the predictions derived from these hypotheses. If males escort their mates to guard them from predation (Power 1980), or if male surveillance results from pair bonding (Lumpkin et al. 1982), following should increase as the season progresses. Instead, we found that male following was most frequent during the fertile period. If males follow females primarily for copulatory access (Gowaty and Plissner 1987), most following should occur in the early morning, when copulation is most likely (Birkhead et al. 1987); instead, male following was consistently high throughout the fertile period, although we performed half the nest watches after 11:00 h. Male surveillance may, of course, serve more than one function (e.g., Power 1980), but our findings are most consistent with the mate guarding hypothesis: males attempt to defend paternity by closely following their fertile mates (Beecher and Beecher 1979, Birkhead 1979).

We found evidence that male Great Crested Flycatchers defend larger territories while their mates are fertile. This evidence should be interpreted cautiously, however, in light of the small sample sizes. The idea that territoriality functions as a form of mate guarding (Møller 1990) is more controversial than that of close following. Although a large territory should increase the average distance between the resident female and intruding males, by patrolling a large territory a male also increases the distance between himself and his mate

(Dunn 1992). Furthermore, if female Great Crested Flycatchers solicit extra-pair copulations outside the territory (e.g., Smith 1988), territoriality is unlikely to have a mate-guarding effect. In some species, there appears to be a trade-off between mate guarding and territory defense (Sherman and Morton 1988, Meek and Robertson 1994); mate guarding by close following may preclude mate guarding through territoriality. It is clear that male Great Crested Flycatchers closely follow their mates during the fertile period. It remains to be determined, however, whether males also use territory defense as a mate guarding tactic. At this time, the relationship between defending territories and defending mates per se is an open question.

Acknowledgments.—We thank K. F. Conrad, P. A. Gowaty, S. A. Hatch, E. D. Ketterson, S. A. MacDougall-Shackleton, H. W. Power, D. F. Westneat, and an anonymous referee for comments on earlier versions of this manuscript. The Queen's Univ. Biological Station provided logistic support. The study was funded by an NSERC Operating Grant to RJR and an NSERC Undergraduate Research Award to EAM-S.

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Wilson Bull., 107(4), 1995, pp. 761–762

Red imported fire ant predation on Crested Caracara nestlings in south Texas.—In 1989 I observed two instances of red imported fire ant (*Solenopsis invicta*) predation on newly hatched nestlings of Crested Caracara (*Caracara plancus*) in the vicinity of the Attwater Prairie Chicken National Wildlife Refuge (APCNWR), Colorado County, Texas (29°40′N, 96°15′W). The refuge encompasses 3232 ha of prairie, marsh, cropland and riparian forest and is kept in secondary succession for habitat for the endangered Attwater's Prairie Chicken (*Tympanuchus cupido attwateri*).

A lone caracara chick hatched in Nest 1 and two chicks hatched in Nest 2 on 16 July and 23 July 1989, respectively. Both nests were built 20 cm below the canopy in Macartney rose (*Rosa bracteata*), approximately 2 m above the ground. On the morning of 16 July I checked Nest 1. The male was perched on a nearby Macartney rose and the female was on the nest. Both adults flew when I climbed the nest tree. I found one live day-old chick and the remains of what appeared to be an unfertile egg (egg yolk, shell fragments) at 08:30 h CST. I observed fire ants on shrub branches near the nest. The adults returned to the nest as soon as I left the area. I returned to the nest in the late afternoon and observed the adults in the same positions as in the morning. I climbed the nest tree again and found the chick dead in the nest covered with fire ants at 16:00 h. I retreated to my truck and at 17:00 h CST saw the female fly to the nest. In a few minutes shew flew off with the dead chick in her bill and dropped it approximately 100 m from the nest. The adults remained in the natal area for another five days, usually perched on shrubs near the nest tree. After 21 July the adults were not seen again. On the afternoon of 23 July I checked Nest 2 for hatching. I found two dead one-day-old chicks in the nest covered with fire ants. The adults perched near the nest but did not appear to enter the nest that day. I returned to the nest on July 24, but was not able to locate the adults. Later observations suggest that the adults abandoned the nest.

I observed five caracara pairs hatch first clutches during the period January–March, 1989, but I found only two clutches in June. Both of these were preyed upon by fire ants. Fire ants apparently were not active during the colder weather in January, February, and March (maximum temperatures of 18.7°C, 14.6°C, 21.8°C, respectively), and cold probably restricted the ants' movements. Porter and Tschinkel (1987) found red imported fire ant workers foraged from 15° to 43°C, with maximum rates between 22° and 36°C. Porter (1988) reported red imported fire ant colony growth ceased below 24°C.

Predation by red imported fire ants on newly hatched chicks has been reported for Northern Bobwhite (*Colinus virginianus*) (Stoddard 1931), Wood Ducks (*Aix sponsa*) (Ridlehuber 1982), Cliff Swallows (*Hirundo pyrrhonota*) (Sikes and Arnold 1986), and colonial water-

birds (Drees 1994). Ridlehuber (1982) reported fire ants destroyed three of 20 clutches in Wood Duck nest boxes. Sikes and Arnold (1986) reported that nesting success with fire ants was 40.5%, compared to 74.9% for nests without ants. Drees (1994) found no fire ant mortality of hatchling waterbirds in late February to mid May, but observed 100% mortality of nests monitored during June and July. Information on ant predation on a raptor is limited to a report by Parker (1977) on Mississippi Kite (*Ictinia mississippiensis*) nestlings. Parker (1977) found three kite nests out of 400 had nestlings preyed upon by native ants of the genus *Monomorium*.

Acknowledgments.—I thank the personnel at the APCNWR and numerous volunteers for field assistance and cooperation. I also thank K. Arnold, J. Morrison, and D. Carrie for their helpful comments on the manuscript, and S. Vinson for information on fire ants. I thank the APCNWR for providing housing and transportation. This study was funded from grants from the Feliciana Corporation, International Research Expeditions, and the Texas Ornithological Society.

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Wilson Bull., 107(4), 1995, pp. 762–764

Food delivery and food holding during copulation in the Loggerhead Shrike.—Copulation in mated birds sometimes is accompanied by a ritual, including the delivery of food from one member of a pair to the other (e.g., Lack 1940, Calder 1967, Tasker and Mills 1981). Observed copulations in the Loggerhead Shrike (*Lanius ludovicianus*) appear to share the common element of food delivery by the male prior to his mounting the female. The retention of the food by the female during copulation has also been reported. Here, I summarize behaviors associated with six copulation events I observed by Loggerhead Shrikes during 1991 through 1993, and I suggest one possible interpretation of precopulatory food delivery and the subsequent holding of the food during copulation in this species.

I monitored nesting pairs of shrikes in southwest Idaho from the time of pair formation through fledging of young (Woods 1994), but found copulation was usually confined to a brief period prior to clutch initiation; five of the six copulations I observed occurred between two and four days before the onset of egg-laying, and three of those occurred exactly two days prior to laying of the first egg. Copulation was often preceded by foraging by the male. Generally the female, perched prominently and apparently watching the male, would begin wing-quivering and calling, the call sounding like a low "waa" rising slightly to a definite if not abrupt end (Woods 1993). It was my impression that these behaviors were initiated by the female upon seeing the male with food although, conversely, the male may have been foraging in response to the female's calls. Nonetheless, as the female called, the male appeared with food and occasionally called in a fashion similar to that of the female. At that time the female typically flew to another perch, or into a nearby shrub, while one or both birds continued to call. The male followed the female, landed, and presented the food to her in a fashion typical of noncopulatory food deliveries. Having received the food, the female held it in her beak as she lowered her upper body so as to stand horizontally. During this time the male quickly flew behind her, hovered with legs tucked under his body, then dropped his legs onto her back, bringing his cloaca to hers as she deflected her tail to one side. During copulation there was generally little movement by either bird, although the male occasionally flapped his wings briefly, apparently to keep his balance and remain mounted on the female. Several high-pitched "twitters" were also sometimes heard during copulation. Copulations lasted 1 to 3 s; in the 30 s or so following copulation, the male typically perched within 0.5 m of the female, while the female either consumed or impaled the food the male had presented to her. The male was sometimes quiet during this time, but following two of six copulations he sang and displayed emphatically to the female (see Smith 1973 for description of displays). In either case, one or both shrikes usually moved off shortly thereafter, with the female sometimes preening in the following minutes.

The Cactus Wren (*Campylorhynchus brunneicapillus*) copulates as early as 18 days prior to egg-laying (Anderson and Anderson 1973:73), but the timing of copulation in some other passerines is similar to that which I observed for the Loggerhead. Maximum copulation rate in paired Zebra Finches (*Taeniopygia guttata*), for example, also occurs two days prior to the start of egg laying (Birkhead et al. 1989). The Loggerhead Shrike, however, appears to have incorporated courtship feeding, and the holding of the food by the female during copulation, into its copulatory behaviors. Smith (1973) found male shrikes fed the female just prior to copulation in all six instances she observed in Washington, and Scott and Morrison (1990) noted one copulation preceded by the male feeding a lizard to the female, which she held during copulation, on San Clemente Island, California. In New York, Novak (1989) also reported copulation to be accompanied by courtship feeding on several occasions. At least five of the six copulations I observed were preceded by the male presenting food to the female prior to mounting her. This food was always held by the female during copulation, and eaten or impaled by her afterward.

The importance of energy supplied to female birds via courtship feeding varies with bird species (e.g., Tasker and Mills 1981, Wiggins and Morris 1986, Salzer and Larkin 1990). The apparent infrequency of copulations in the Loggerhead (pers. obs.), however, implies that food presented during the copulation event is almost certainly more important from a behavioral than an energetic standpoint (although this may be untrue for general courtship feeding in the species [cf. Carlson 1985]). Why, then, the incorporation of food delivery and, in particular, food holding into copulatory behaviors? Shrikes of the genus *Lanius* are distinct among the passerines owing to the hooked bill and tomial teeth which are used to dispatch the vertebrates upon which they prey, including small rodents, birds, and reptiles (Cade 1967). Consequently, aggression between shrikes has inherent danger, and Smith

(1973) suggested that ritualization of aggressive behaviors in the Loggerhead serves to reduce the possibility of injury to potential combatants. Copulation in several Palearctic shrike species (Great Grey Shrike [*L. excubitor*], Lesser Grey Shrike [*L. minor*], Woodchat Shrike [*L. senator*]) is also sometimes accompanied by food delivery, and aggression toward male Woodchat Shrikes has been noted when copulation attempts have not been preceded by food delivery (Cramp and Perrins 1993). Thus, prey delivery by male shrikes, and the subsequent holding of the food by the female, could result from reluctance by the male to mount the female otherwise, since she may be inclined to peck at him when she is not holding food.

Acknowledgments.—C. Blem, T. Cade, A. Dufty, and R. Yosef provided valuable comments and criticisms of earlier drafts of this manuscript. These observations were made during a study funded in part by Boise State University's Raptor Research Center and a Grant-in-Aid of Research from Sigma Xi.

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Wilson Bull., 107(4), 1995, p. 765

Additional records of owls and wood warblers from México.—In the collection of birds of the Laboratorio de Ornitología, Facultad de Ciencias Biológicas, Univ. Autonoma de Nuevo León (UANL), and Allan R. Phillips (=ARP), we have seven specimens of two species of owls and four species of wood warblers, representing new records for Nuevo León and Aguascalientes. Recently Enriquez-Rocha et al. (1993), in a revision of the distribution of owls in México, included 27 species that occur in all states. They recorded 3683 specimens from museum collections. The wood warblers of Nuevo León, as reported by Miller et al. (1957) include 26 species. Martín del Campo (1959) listed 16 species, and Contreras-Balderas (1973) added Black-throated Gray Warbler (*D. nigrescens*). The new records and their states are:

Burrowing Owl (*Speotyto cunicularia*).—UANL 880, (male). El Milagro, Aguascalientes, Aguascalientes. 11 September 1981. This record is the fifth species of owl from Aguascalientes.

Short-eared Owl (*Asio flammeus*).—UANL 28, El Mezquital, Apodaca, Nuevo León. 18 December 1969. This record increases to 14 the species of owls known from this state.

Yellow Warbler (*Dendroica petechia*).—UANL 506, (adult female). Manantial Las Blancas, 2.5 km E of Mina, Nuevo León, México. 4 September 1971. UANL 1302. (adult male). Parás, Nuevo León, México. 13 May 1985.

Black-throated Blue Warbler (*D. caerulescens*).—UANL 239, (adult male). Las Huertas, Cañon de Meleros, Santa Catarina, Nuevo León, México. 29 December 1971. (Now Delaware Museum of Natural History, DEL 30325).

Prothonotary Warbler (*Protonotaria citrea*).—ARP 11095, (adult male). Presa La Boca, Santiago, Nuevo León, México. 21 May 1977.

Northern Waterthrush (*Seiurus novaboracensis*).—UANL 509, (immature female). Ojo de Agua de Lampazos, Nuevo León, México. 11 September 1971.

The record for *D. caerulescens* is the first report for continental México, previous records being from Isla Cozumel to Central America. Wauer (1973) found this species in west Texas and Oberholser (1974) includes a few more localities from Texas.

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Wilson Bull., 107(4), 1995, p. 766

An unusual record of Sandhill Crane philopatry.—Greater Sandhill Crane (*Grus canadensis tabida*) pairs are well known for their breeding territory fidelity (Walkinshaw, The Sandhill Cranes. Cranbook Institute of Sci., Bloomfield Hills, Michigan, 1949; Littlefield, Breeding biology of the Greater Sandhill Crane on Malheur National Wildlife Refuge, Oregon. M.Sc. thesis, Colorado State Univ., Fort Collins, Colorado, 1968; Drewien, Ecology of Rocky Mountain Greater Sandhill Cranes. Ph.D. Diss., Univ. of Idaho, Moscow, Idaho, 1973). An extreme incident of such fidelity occurred in both 1984 and 1985 along the north shore of Malheur Lake, Harney County, in southeast Oregon. After substantial precipitation associated with the 1982 El Nino Event, Malheur Lake joined with Mud and Harney lakes to create the largest Oregon inland water body, covering about 72,875 ha. During the flood, marsh and meadow habitats which adjoined the lake became totally inundated, resulting in the submergence of 17 *G. c. tabida* breeding territories.

By spring 1984, these territories were under a large expanse of open water, and other than a few ranch buildings and trees, the only exposed objects were several isolated haystacks. During an aerial waterfowl survey in early June 1984, an incubating Greater Sandhill Crane was observed flying from a nest on a haystack about 3.2 km from shore. Although it appeared the crane pair successfully hatched their 2 eggs, no young were known to have survived. Though young cranes are capable of swimming, it would have been highly improbable that these chicks would have been able to swim to the shoreline.

Lake levels continued high in 1985, but haystacks were beginning to disintegrate and several small uplands had appeared near the north shore; however, the crane pair again nested at the haystack site. In addition, other pairs were nesting on newly exposed or nearly exposed uplands. From an airboat we visited the haystack site as well as two upland sites on 25 June 1985. Following is a description of nests located at these sites.

Nest 1 was at the disintegrated haystack on a mat of floating smartweed (*Polygonum aquatilus*) over unmeasured deep water. Both eggs had hatched, but the nearest dry land was about 3.2 km northeast. As no islands were between the nest and the shore, it was most likely both chicks drowned before reaching a dry site. Nest 2 was located on a nearly submerged upland among black greasewood (*Sarcobatus vermiculatus*), about 1.6 km into the lake. The site was in newly established smartweed. Both eggs had hatched by 25 June, but no young were present; however, on a nearby island about 0.4 km north of the nest site a dead adult male crane was discovered, but it was not known if he was a member of the nesting pair. Nest 3 was a new nest with eggs having been laid between 15–20 June. The site was on a small island covered with water-killed greasewood about 0.4 km from shore. Interestingly, this was the latest crane nesting effort ever recorded in the Malheur-Harney Lakes Basin, Oregon, since studies were initiated in 1966.

To our knowledge, such a strong incident of Greater Sandhill Crane philopatry has not been previously reported, nor is there a record of sandhill cranes nesting on a haystack. Adequate unoccupied nesting habitat was available both north and northwest of the lake in both 1984 and 1985, but at least some pairs selected to remain at their traditional breeding territories even though these sites were submerged. It is believed that philopatry arose from the advantage which individuals gain from increasing familiarity with an area (Campbell and Lack, A dictionary of birds. Buteo Books, Vermillion, South Dakota, 1985), but in this event philopatry was certainly a disadvantage for successful reproduction.

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Wilson Bull., 107(4), 1995, pp. 767–768

Ghost crab preys on Piping Plover eggs.—The Piping Plover (*Charadrius melodus*) is endemic to North America and breeds locally on the Great Plains, Great Lakes region, and upper Atlantic Coast (Haig 1992). By 1900 this species was near extinction primarily due to unregulated market hunting. Protection under the migratory bird treaty act allowed for a short recovery period which peaked in the 1930s (Haig and Oring 1985). Since 1945, however, Piping Plover populations have been declining due to modification of nesting habitat, human disturbance on the few remaining nesting grounds, and an apparent rise in nest predation (Haig 1992, Haig and Plissner 1993). Currently, Piping Plover populations in Canada and in the U.S. Great Lakes region are considered endangered (Haig 1985) and populations on the Atlantic Coast and Great Plains are considered threatened (U.S. Fish and Wildlife Service 1985, Haig 1985). For this reason, identification of factors causing nest failure are of interest.

On 4 June, 1994 while conducting an annual survey for Piping Plovers along the Virginia Barrier Islands, we observed a pair of plovers displaying unusual behavior. The pair was within a series of low, remnant, dunes, approximately 60 m from a small Little Tern colony (*Sterna albifrons*). Upon our approach, the plovers gave the normal series of calls and distraction displays. However, as we withdrew, the pair began to move back and forth between two or three locations on the beach, and continued to display for approximately 10 min. As we approached the central location, we observed a well formed nest cup with a deep burrow positioned in the center. A ghost crab (*Ocepode quadrata*) was partially visible within the burrow. In order to determine the nest contents we excavated the burrow to a depth of 0.5 m (the end of the burrow was never reached). Two broken, but uneaten Piping Plover eggs were discovered in the burrow. The exposed embryos appeared to be approximately two weeks old. Given the behavior of the pair and the fresh condition of the eggs, we believe that the eggs had been taken just prior to our arrival.

Predation has been identified as one major factor limiting reproductive success in Piping Plovers (e.g., Gaines and Ryan 1988, MacIvor et al. 1990, Patterson et al. 1991). Ghost crabs may be one of many predators reducing fledging success in this species (U.S. Fish and Wildlife Service 1995). Depredated chicks have been found in and around ghost crab burrows (R. Cross, pers. commun.). Young chicks (<2 wks old) are apparently vulnerable to predation at night when ghost crabs are most actively searching for food on the beach surface. However, we are unaware of previous suggestions that ghost crabs may recognize unhatched eggs as prey items. We have examined well over 500 Piping Plover nests since 1986. This represents the first observation of egg predation by ghost crabs that we have detected.

Acknowledgments.—R. Cashwell and B. Truitt provided boat transportation to the islands. The Virginia Dept of Game and Inland Fisheries, Nongame and Endangered Wildlife Program provided financial support. S. Haig and C. R. Blem made helpful comments on an earlier draft of this manuscript.

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Wilson Bull., 107(4), 1995, pp. 768–769

Ghost crab preys on a Piping Plover chick.—East Coast Piping Plovers (*Charadrius melodus*) were listed as threatened because of declining populations (Fed. Register 1985) due to loss of habitat and human disturbance. Predation of nests and young has been cited as one cause of the decline (Fed. Register 1985, Dyer et al. 1988, Melvin et al. 1991, Haig 1992). Here we describe predation of a Piping Plover chick by a ghost crab (*Ocypode quadrata*) on Assateague Island National Seashore, Maryland.

On 7 July 1988, 08:45 EDT, JPL and LLL approached a brood of two 8-day-old Piping Plover chicks and two adults to complete behavioral observations (Loegering 1992). From >70 m, we observed the birds moving along the beach. Both chicks appeared healthy. One adult alarm-called when we initially approached; however, after we sat and remained motionless (<2 min.) it appeared undisturbed. As the brood moved along the beach, the adults suddenly became alarmed and ran down the beach. We observed the brood for 13–15 min. but only saw one chick. We then walked toward our vehicle on the ocean tidal zone. As we crossed the path previously taken by the brood, we discovered a freshly killed plover chick 0.1 m from a ghost crab burrow. The chick had a laceration from the sternum to the pelvis, and much of the viscera was displaced or missing. The blood present was very wet and bright red. It weighed 9 g (partially eviscerated). We retreated 25 m and a ghost crab emerged from its burrow after approximately 3 min. We photographed the crab feeding on the chick. We dug the ghost crab out of its burrow, measured it, and released it unharmed (weight = 42.5 g, dorsal carapace width = 41 mm, dorsal carapace length = 32 mm).

We did not directly observe the ghost crab attack the chick; however, we feel very confident that this chick was the second from the brood we observed minutes earlier. We intensively searched for and monitored nests and broods daily (Loegering 1992). The closest adjacent plover brood was >500 m away, and contained two chicks that were accounted for before and after our observations. Additionally, we color-banded the remaining chick

from this brood the following day, and relocated this chick daily until it fledged. We never observed an additional chick.

To our knowledge, this is the only report of ghost crab depredation of a Piping Plover chick. In a similar instance, Patterson (1988) reported adults repelling a ghost crab that "seized a recently hatched chick." Since 1988, other researchers have expressed concern that ghost crabs may be affecting plover nest site selection and/or productivity as far north as New Jersey (U.S. Fish and Wildl. Serv. 1995). In 1994, a preliminary study to assess the extent of ghost crab predation on plover eggs and chicks was conducted on Chincoteague National Wildlife Refuge, Virginia; however, the results indicated that ghost crabs were not as important at that site as previously thought (T. Wolcott, pers. comm.). While our observation confirms that ghost crabs will prey upon Piping Plover chicks, further study is needed to determine if our observation was an isolated incident or if crabs are frequent predators of plover chicks.

Acknowledgments.—We thank the National Park Service and Maryland Natural Heritage Program for funding this study.

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John P. Loegering, James D. Fraser, and Lisa L. Loegering, *Dept. of Fisheries and Wildlife Sciences, Virginia Polytechnic Inst. and State Univ., Blacksburg, Virginia 24061-0321 (Present address JPL and LLL: Oregon Cooperative Wildlife Research Unit, Dept. of Fisheries and Wildlife Sciences, 104 Nash Hall, Oregon State Univ., Corvallis, Oregon 97331-3803).* *Received 7 Feb 1995, accepted 1 May 1995.*

Wilson Bull., 107(4), 1995, pp. 770–775

ORNITHOLOGICAL LITERATURE

Edited by William E. Davis, Jr.

Trends in Geographic Variation of Cooper's Hawk and Northern Goshawk in North America: a Multivariate Analysis. Proceedings of the Western Foundation of Vertebrate Zoology, Vol. 5, No. 3. By Wayne H. Whaley and Clayton M. White. Western Foundation of Vertebrate Zoology, Camarillo, California. 1994:161–209 pp., 22 numbered maps and figs., 10 numbered tables. $8.00 (paper).—Subspecies are no longer "popular" in North American ornithology, and studies of geographic variation in avian anatomy are not as common as they once were. Indeed, the most recent previous accounting of geographical variation in North American accipiters was published almost a quarter of a century ago (Wattel, J. Geographical differentiation in the genus *Accipiter*. Nuttall Ornithological Club, Cambridge, Massachusetts, 1973). Whaley and White's substantial and significant contribution helps right this unfortunate wrong.

After an introduction that correctly concludes that studies such as the authors' offer fertile grounds for testing both physiological and ecological theory, the authors detail the results of a painstaking analysis of geographic variation in the anatomical features of more than 1200 museum specimens of Cooper's Hawks (*Accipiter cooperii*) and Northern Goshawks (*A. gentilis*) collected during the breeding season. Reverse sexual size dimorphism is considerable in accipiters, and Whaley and White analyze their data both within (female versus male) and across species. After presenting their results, the authors conclude with a discussion that encompasses numerous physiological and ecological hypotheses, including Bergmann's and Allen's rules, competition theory, and the results of many regional studies of the diets, breeding ecology, and migration behavior of the two species. Building upon a strong foundation of natural-history information, Whaley and White's results and discussion offer considerable food for thought.

As might be expected, the more migratory Cooper's Hawk (with two recognized races) exhibits less geographic variation, overall, than the more sedentary Northern Goshawk (with five recognized races in the region). Even so, the two species exhibit considerable concordance in their geographical trends, as do males and females within species. In both Cooper's Hawks and Northern Goshawks, individuals from southwestern locations are larger than birds elsewhere, a phenomenon the authors attribute both to physiological (e.g., reduced water stress) and ecological (e.g., enhanced competitive ability in the face of incursions from more northerly migrants) forces. The authors go on to suggest that the smaller size of birds in the northwestern United States reflects an adaptation for maneuverability in the dense rain forests they inhabit there. Geographic shifts in the relative importance of avian prey in the diets of the two species are used to explain why Cooper's Hawks have longer toes in the east, and goshawks shorter toes in Alaska. The fact that goshawks east of the Rockies are more migratory than their western counterparts is used to explain why the former have more pointed wings than the latter. A similar argument is made for both wing shape and wing loading in eastern versus western Cooper's Hawks. The results are compared with additional data on Sharp-shinned Hawks (Smith, J. P. 1988. Morphometric variation in accipiter hawks with emphasis on western North America. Unpublished M.S. thesis, Utah State University, Logan, Utah), with Whaley and White concluding that the high degree of concordance existing among the three species reflects similar selection pressures.

Although Whaley and White assemble convincing cases for most of their conclusions, I could not help but wonder if recent ecological and evolutionary forces may have contributed to several of their findings. The museum specimens used by the authors were collected over

a period of more than 100 years, a time of considerable ecological upheaval for North American raptors. Populations of many species, especially accipiters, were reduced significantly during this time, both as a result of the wholesale destruction of the birds' forested habitats, as well as the methodical shooting of masses of birds at traditional migratory bottlenecks. The extent to which such acute selective forces have acted to, quite literally, shape the geographic ecology and anatomy of the birds in question remains an unstudied topic.

The above is but one example of the food for thought Whaley and White's analysis serves up for the reader. The authors, together with the Western Foundation of Vertebrate Zoology, are to be congratulated for publishing this major contribution to the raptor literature. I highly recommend it, both for its content and potential use as a role model in similar studies.—Keith L. Bildstein.

Moult and Ageing of European Passerines. By Lukas Jenni and Raffael Winkler. Academic Press, London and San Diego, 1994: 225 pp., 652 figures (mostly color photographs of spread wings and diagrammatic representations of molt stages). $40.00.—The first thing that must be said about this oversized (24 × 31 cm) book is that it could only have been done in Europe. The authors are Swiss, and the data for the book were collected over many years at the banding station at Col de Bretolet in the Swiss Alps and at the Natural History Museum in Basel. There are simply no individuals or teams in North America with a sufficient data base, background knowledge, and, alas, interest in molt to be able to produce a comparable tome for New World passerines. I would love to be wrong about this.

The book is in two parts, each with several chapters. The first chapter is an exceptionally thorough introduction to plumage and the role of molt in the life history of a bird. This is followed by a chapter entitled "The terminology of feathers, plumages, moults and age classes." I was happy to see that they advocate numbering the primaries descendently (i.e., from inside to outside). They point out that "papers describing exceptional moult patterns are still presented without giving [the] vital information" as to which numbering system was used. The authors somewhat grudgingly admit that "A terminology based on homologies of plumages and moults would certainly be desirable and has many advantages (Humphrey and Parkes 1959 [Auk 76:1–31], 1963 [Auk 80:496-503], Rohwer et al. 1992 [Condor 94:297–300])." However, in defense of their failure to adopt the concepts and resultant terminology of Humphrey and Parkes, they point out that there are numerous Palearctic passerines that have evolved unusual molt cycles. These have been studied purely descriptively, and not in any phylogenetic or evolutionary context that would clarify homologies; Humphrey and Parkes (1959, 1963) admitted that apparent exceptions to the widely prevalent and easily homologized molt cycles would take special study. Such studies being lacking, Jenni and Winkler therefore revert to a molt terminology based on the reproductive cycle. In accordance with their rather defeatist desire for simplification, they have taken the position that for long-distance migrants, only the molt prior to fall migration is to be called the "postbreeding/postjuvenile moult," with any subsequent molting in the winter range being attributed to the "prebreeding moult." They are not consistent in this usage, however, as the complete molt of the [Barn] Swallow (*Hirundo rustica*) in the winter quarters is "interpreted as a complete postjuv[enile] moult in 1yr [=first year] and a complete postbr[eeding] moult in ad." They admit that some individual Barn Swallows begin body molt prior to and continue it during migration, finishing it in the winter range, but it is the wing molt alone that determines their terminology.

Chapter 3 is a detailed account of the molt strategies of adult passerines, illustrated with

diagrams and graphs that take a bit of study to comprehend. Much attention is paid to variations from the commonest patterns, with examples, and there is a detailed discussion of the great variation in sequence and timing of molt in trans-saharan migrants, a variation that appears to be without counterpart in Neotropical migrants. Chapter 4 is an even longer discussion of molt patterns in the first year of life.

Part II begins with a chapter on techniques for ageing European passerines using plumage and molt characters; skull pneumatization is described and figured in an appendix. Ageing by rectrix shape, useful in so many American species, is barely mentioned on p. 50 as a possibility, but is not pursued further.

The body of the book is devoted to descriptions and figures (both color photographs and diagrams) of the wing molt of (only) 58 species of European passerines, with the emphasis on age determination. Areas of the plumage other than the wing are usually briefly mentioned if they are pertinent to age determination. The approximately 480 photographs of spread wings are carefully labelled as to date, age of the bird, and the stage of molt or wear that indicates the age.

The species accounts, the largest part of the book, are clearly intended for use by banders, although a few museum curators will want to apply the criteria to ageing specimens; in the case of remiges, this will not be easy unless the skin has been prepared with one wing spread.

The book ends with an extensive bibliography, a list of scientific names with their English, German, French, Italian and Spanish equivalents, a species index, and a page (224) of "Explanation," which includes lists of abbreviations, a diagram of names and numbers of wing feathers, and examples of diagrams used in the text. An unnumbered p. 225 is identical to 224, and the authors suggest that this be cut out and used as a book mark; not a bad idea, considering the number of abbreviations used and the strangeness of some of the diagrams.

The authors, of course, know that remex is the singular of remiges (you'd be surprised at the number of people who think it is "remige"), but fail to recognize the parallel singular "phalanx," referring on p. 7 to "the first phalange [*sic*] of the second digit."

The species accounts as such will be of only peripheral interest to American banders except for the few species, such as the [Barn] Swallow, Sand Martin [Bank Swallow] (*Riparia riparia*), [Common] Redpoll (*Carduelis linaria*), and [Red] Crossbill (*Loxia curvirostra*) that are found on both sides of the Atlantic. The introductory parts of the book, however, would make quite a good initiation to molt and ageing studies for the many ornithologists unfamiliar with these aspects of avian biology.—Kenneth C. Parkes.

La Selva, Ecology and Natural History of a Neotropical Rain Forest. Edited by Lucinda A. McDade, Kamaljit S. Bawa, Henry A. Hespenheide, and Gary S. Hartshorn. The Univ. of Chicago Press, Chicago, 1994: 486 pp., 10 halftones, 17 maps, 69 line drawings, 79 tables. $28.95 paper, $90.00 cloth.—La Selva is a nature reserve and biological station of the Organization for Tropical Studies, which is adjacent to Braulio Carrillo National Park in the Atlantic lowlands of northeastern Costa Rica. This volume provides a comprehensive review of over 30 years of research in one of the most intensively studied tropical field sites in the world. The book includes 26 chapters organized into sections on the abiotic environment, plant and animal communities, plant-animal interactions, and the impact of land use and forestry and agricultural development on La Selva and other areas of Costa Rica. Appendices contain species lists of vascular plants and vertebrates. The list of birds of La Selva and vicinity includes information on abundance, seasonal status, habitat,

and recent changes. The authors synthesize information in their subject areas, compare La Selva to other tropical research sites, and identify gaps in knowledge, which are often gaping in tropical systems. Plant biology and vegetation dynamics have been best studied at La Selva, whereas little is known about the ecology of La Selva birds. Invertebrate biology (with the exception of butterflies) and aquatic ecology have received little study until recently. This book is written primarily for tropical researchers and ecologists, but much of it should be comprehensible to serious natural history tourists. It is a valuable resource for researchers at La Selva and other neotropical sites.—Sue A. Perry.

Raptor Conservation Today. World Working Group on Birds of Prey: Proc. 4th World Conference. Edited by B.-U. Meyburg and R. D. Chancellor. 1994:816 pp. $49.95.—An international conference on birds of prey held in Berlin in 1991 attracted more than 500 participants with strong representation from eastern Europe, the Balkans and the components of the former USSR. One hundred of the presentations have been gathered into this large volume. Even so, a smaller one, due this year, will contain those relating to eagles. The cover of this volume is a color photograph of that most spectacular of birds of prey (in size and appearance, if not in behavior)—Steller's Eagle (*Haliaeetus pelagicus*). Excellent sketches of various species by F. Weick are scattered throughout the text. The overall emphasis, as would be expected, is on conservation, management, and status, but investigators, whatever their goals, will profit from the treatment of such subjects as radiotagging and the pitfalls thereof by R. E. Kenward and S. S. Walls. The papers are grouped under ten natural headings concluding with 17 on the inroads of pesticides and poisons. Some contributions relate entirely and others in part to basic research. The longest and most detailed paper, for example, is a taxonomic revision of the entire order Falconiformes (R. N. Holdaway). Others analyze the effects of food supply and nesting success on molt in Tawny Owls (*Strix aluco*), genetic fingerprinting in Eleonora's Falcon (*Falco eleonorae*), and DNA analysis of the species of the genus *Falco*. In short, this volume, with its many included bibliographies, provides a cross-section of current work on the biology, management and conservation of hawks and owls.—Dean Amadon.

Conservation and Management of Neotropical Migrant Landbirds in the Northern Rockies and Great Plains. by David S. Dobkin. Univ. of Idaho Press, Moscow, Idaho. 1994: 220 pp., 144 range maps, 6 numbered text figures, 3 tables. $29.95 (paper).—Concern over declining populations of many Neotropical migrant birds has engendered much interest, research, controversy, and several symposiums on the problem in recent years. Most of the work has been from the eastern United States, so this work that summarizes the current state of knowledge for a western region is most welcome.

The book is an extension of a report for the U.S. Forest Service, Region 1, and includes all of Montana and North Dakota, the northern half of Idaho, and northern parts of Wyoming and South Dakota. Figures show the distribution of U.S. Forest Service, Fish and Wildlife Service, and National Park Service lands, and the physiographic regions of the Northern Rockies and Great Plains. The introductory section reviews the literature and arguments over the two major factors contributing to the decline of Neotropical migrant populations—forest fragmentation on the breeding grounds in the United States, and deforestation and other problems on the wintering grounds in the Neotropics. The North American Breeding Bird Survey (BBS) is discussed as the major data base for monitoring long-term population

trends, and the paucity of BBS data in many areas of the west is cited as one reason that less is know about western Neotropical migrant birds. The data do suggest, however, that Neotropical migrant birds in the west are doing better than those in the east. One explanation offered is that most forest fragmentation in the west is due to timber harvest, and hence the land retains the potential of returning to second-growth forest; another is that western migrants tend to use different parts of the Neotropics from eastern birds. The author emphasizes the desperate need for more long-term studies in the west, and argues for a species-level research focus combined with a habitat-based conservation effort.

The second part of the book surveys management activities and their impacts. The survey is divided into three sections, coniferous forests, deciduous forest, and grasslands and shrub-steppe, and reviews the state of knowledge (including a review of the literature) for each of the major plant communities (e.g., Douglas fir and ponderosa pine, riparian woodlands, aspen woodland, shortgrass, mixed-grass, tallgrass prairie). In addition the author considers the effects of livestock grazing, fire and its suppression, pest management, and provides a summary and recommendations.

The bulk of the book (150 pages) is devoted to the 144 species accounts of Neotropical migrant birds which breed in this region. Three tables detail each species' distribution in twelve major habitat types, and wintering area in the Neotropics (e.g., winters exclusively in South America). The accounts are short—one per page—and are meant to provide a synopsis of the most pertinent information concerning the species' conservation and management, and are intended to be of heuristic value. Each account provides seasonal residency status, wintering area, habitat requirements, food and foraging techniques, population status (regional, western, and continent-wide trends), management, recent literature, and a range map.

This book is a valuable resource. Its more than 650 references (most recent 1993) may alone be worth the price of the book. I would like to have seen winter range maps for each species rather than a code number which referred to a key on the first page of the species accounts, but this is a minor quibble. This book should be of interest to anyone interested in Neotropical migrant birds, or the distribution and ecology of western birds.—William E. Davis, Jr.

Disturbance to Waterfowl on Estuaries. By Nick Davidson and Phil Rothwell (eds.). Wader Study Group Bulletin 68, Special Issue, August 1993. Obtain from: Policy Operations Department, The Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, U.K. £15, postage and handling included (paper).—Recreational use of coasts and estuaries is creating problems for wildlife in many places around the world, including North America. Hence this book, a compendium of 16 papers involving disturbance to a wide variety of birds which inhabit estuaries, is timely and important. It is the outgrowth of a 1991 conference sponsored by the Nature Conservancy Council and The Royal Society for the Protection of Birds. Although the papers deal with problems of disturbance in the estuaries of north-west Europe, they mirror problems of the coasts and estuaries of North America.

The papers deal with a wide variety of "disturbances." These include the elimination of habitat through development of marinas, housing, and leisure complexes, and the disturbance of feeding or roosting birds by hunting, boating, water-skiing, walking along beaches or mudflats, dogs, 4-wheel drive RVs, airplanes, and helicopters. Some papers present previously unpublished research; other papers summarize what has been previously published. Some papers are theoretical, others descriptive or experimental. Some deal with a single

species, e.g., Eurasian Widgeon (*Anas penelope*), Kentish Plover (*Charadrius alexandrinus*); others deal with a broad spectrum of gulls, ducks, and shorebirds (Charadriidae, Scolopacidea). One chapter consists of summaries of published papers and reports outside the scope of this book, including summaries of four papers reporting on North American studies.

Aside from the sometimes confusing and overlapping usage of the terms "waterfowl," "waders," and "shorebirds," I found the papers interesting and informative. The book should be of interest to anyone concerned with anthropocentric disturbance, or the ecology and management of estuarine habitat.—William E. Davis, Jr.

The Biology and Status of the Long-billed Corella in Australia. by W. B. Emison, C. M. Beardsell, and I. D. Temby. Proc. West. Found. Vert. Zool. 1994, 5:211–247. 24 numbered text figs., 1 table. $7.00.—This monograph reports on an exhaustive study of the Long-billed Corella (*Cacatua tenuirostris*) in southeastern Australia. Although the stated aims of the study were to collect information on seasonal distribution, flocking behavior, habitat preferences and other activities of this species, this report does much more—it provides a thoroughly researched and documented history of a bird which suffered severe ecological repercussions from interactions with humans.

The corella probably benefitted from the fire regime of the aborigines, since the fires promoted the development of grasslands and grassy woodlands. But the advent of European settler/pastoralists with their sheep, beginning in 1837, caused the rapid disappearance of the corella's primary food resource, the plant murnong. European settlement along the rivers, where cattle and sheep destroyed weedbeds, severely restricted another of the corella's seasonal food resources (aquatic plant roots). Crop damage by corellas soon brought on retaliation by gun and poison. By 1860 the numbers and range of Long-billed Corellas had been severely reduced. The final ecological disaster perpetrated by man followed the explosive growth of the introduced rabbit population. This led to a further, gradual, decline in corella numbers from 1860 to the 1950s when the introduction of myxomatosis eliminated most of the rabbits, and with them intense competition for food, a defoliated landscape, and the farmer's poisoned grain. Since then the recovery of the corellas has been steady, and their range has rapidly expanded, despite increasing conflict with farmers whose crops are a major corella food resource. More than 90% of the diet of Long-billed Corellas consists of introduced plant species.

This study, conducted by the Dept. of Conservation and Natural Resources of Victoria from 1978–1984, included wing-tagging 704 corellas, and produced a wealth of detailed natural history information, including a study of molt. All aspects of breeding biology were studied, and included, for example, studies of nest attendance at nests with tagged birds. Feeding studies included analysis of the contents of 314 stomachs, with onion grass (an alien species) corms and oat grains the predominant food, although seasonal shifts in food resources were considerable. Long-billed Corellas are relatively sedentary, with more than 85% of sightings of tagged birds within 5 km of where they were tagged. Other results detail flocking size and behavior, and mortality ("shot by farmers" was a leading cause of death). The habitat descriptions and analyses, including important plant associations such as the river red gums which are prime breeding habitat, are a major part of this report. They include the distribution of onion grass and the various agricultural crops upon which the corellas depend.

This is a well researched, well written, and informative monograph about a resilient cockatoo species. The history of its interactions with man are fascinating. I recommend this monograph to anyone interested in avian conservation, particularly for its historical perspective.—William E. Davis, Jr.

Wilson Bull., 107(4), 1995, pp. 776–789

PROCEEDINGS OF THE SEVENTY-SIXTH ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Seventy-sixth Annual Meeting of the Wilson Ornithological Society was held Thursday, 4 May through Sunday, 7 May, 1995 at the Fort Magruder Inn and Conference Center, Williamsburg, Virginia in joint session with the Virginia Society of Ornithology. The local committee, chaired by Ruth Beck, was composed of Bill Akers, Joy Archer, Jean Armour, Tom Armour, Sherwin Beck, Jean Holcombe, Marilyn Lewis, Carolyn Lowe, Mack Lundy, John McDowell, Charles Rend, Jean Rend, David Schuster, Lee Schuster, Mary Smith, Alice Springe, Brian Taber, Jerry Via, Dorothy Whitfield, Bill Williams, and Marilyn Zeigler. The meeting was sponsored by the Dept. of Biology of the College of William and Mary, the Virginia Dept. of Game and Inland Fisheries, the Virginia Society of Ornithology, and the Williamsburg Bird Club.

The Council met from 13:08 to 18:30 on Thursday, 4 May in the Longstreet Redoubt and again from 17:00 to 17:15 on Friday, 5 May in Newmarket Hall. On Thursday registration for the approximately 175 guests and members was followed by an informal reception at the General Hill and General McClellan Redoubts.

The opening session on Friday convened in Newmarket Hall at 08:20 with welcoming remarks from Bill Akers, president of the Virginia Society of Ornithology, Ruth Beck, president of the Williamsburg Bird Club, and Stan Sadler, vice-president of the College of William and Mary. Professor Mitchell Byrd of the Center for Conservation Biology and the Dept. of Biology at William and Mary College provided an enlightening review of colonial ornithology in the Williamsburg area. Richard Conner, president of the Wilson Ornithological Society, offered a response to this most warm and well-received welcome.

The scientific papers session included contributed papers and posters as well as a symposium on Ornithology in Northern Central America. The evening program on Friday offered a delightful audio-visual presentation, "Nature's Jewels," by Dr. Hal Horwitz. After the business meeting of the Virginia Society of Ornithology, all members and guests enjoyed an informal reception. Field trips to local areas were conducted on Friday, Saturday, and Sunday mornings, while additional extended field trips on Sunday took members and guests to a variety of habitats in coastal Virginia.

A social hour preceded the annual banquet held in General Hill and General McClellan Redoubts. Following dinner, President Conner reinstituted the brief president's address to the Society. The following awards were also presented:

EDWARDS PRIZE (for the best major article in volume 106 of *The Wilson Bulletin*)

Bret M. Whitney, "A new *Scytalopus* Tapaculo (Rhinocryptidae) from Bolivia, with notes on other Bolivian members of the genus and the *Magellanicus* complex." Wilson Bull., 106 (4):585–614.

LOUIS AGASSIZ FUERTES AWARD

Dan Albrecht, "Sex ratio variation in nests of first- and second-paired female House Wrens."

MARGARET MORSE NICE AWARD

David J. Ziolkowski, Jr., "The role of male song in territorial defense: an experimental test using House Wrens."

PAUL A. STEWART AWARDS

Daniel R. Ardia, "Habitat selection and sexual segregation in American Kestrels."
Jeanette Bider, "Avian diversity and distribution among remnant forests of North-central Belize."
Jeffrey P. Duguay, "Effects of two timber management practices on arthropod abundance and towhee nestling growth rates."
Megan E. Laut, "Demographic responses of Carolina Chickadee to forest fragmentation."
Winli Li, "Parental behavior and possible brood-splitting in Whimbrels (*N. phaeopus*).
Todd J. Underwood, "The validity of constant effort mist-netting in generating a reliable index to productivity."

ROGER TORY PETERSON INSTITUTE TRAVEL AWARD

John N. Mager, "Parental effort in the seasonally monogamous Common Loon (*Gavia immer*)."
Jameson F. Chace, "Cowbird parasitism and nest predation on Solitary Vireo nests: does nest choice make a difference?" and "Nest-site selection by Solitary Vireos."

ALEXANDER WILSON PRIZE (for best student paper)

Amanda Allen, "Tidepool value as foraging patches for breeding and migrating birds in tidal salt marshes in the Lower Chesapeake Bay."

Selection committee for the Edwards Prize—Charles Blem, chair, Al Conway, Danny J. Ingold, Steven L. Lima, Lisa J. Petit, and Stephen Pruett-Jones; for the Fuertes, Nice, and Stewart Awards—Judy McIntyre, chair, Gary Nuechterlein and Richard Stiehl; for the Wilson Prize—Jon Barlow, chair, John Kricher and Clait Braun; for the Peterson Institute Travel Award—Keith Bildstein, chair, John Smallwood and Dan Petit.

Banquet festivities concluded with a film presentation, "Watching Warblers," by Mike Male and Judy Fieth.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Conner at 08:35 on Friday, 5 May in Newmarket Hall. Secretary Zimmerman reviewed the highlights of Thursday's Council meeting, noting that the current membership stands at 2410. He reported that the council acted in response to a recommendation of the publications committee, chaired by Clait Braun, that the Society reinstate an honorarium for the editor. The council also reelected the editor for another term. Efforts of the Ornithological Council were reviewed, and Zimmerman reported that the Society has designated that rental income on the membership list collected by OSNA would be used to support the Ornithological Council as well as again providing a $500 contribution from our general funds for the coming fiscal year. The Committee on Undergraduate Outreach, chaired by Ernest Willoughby, has the information exchange available on Internet and is preparing a guide to graduate programs in ornithology for undergraduates. The Council voted in favor of our OSNA representative to accept the membership of the Colonial Waterbird Society and the Raptor Research Foundation in

OSNA. The proposed budget for the coming year is around $105,000. Next year's meeting will be hosted by the Cape May Bird Observatory from 11–14 April 1996 at Cape May with Peter Dunne as local chair. In 1997 the Society will meet in Manhattan, Kansas from 17-20 April in conjunction with the Kansas Ornithological Society, hosted by the Division of Biology at Kansas State University. John Zimmerman is local chair. The secretary then asked those assembled to stand in recognition of the following members who have died since we last met: Helen G. Cruickshank (Rockledge, FL), Harvey I. Fisher (Hale, MO), Ernest E. Good (Columbus, OH), E. Hoving (Winnipeg, MB), Marion A. Jenkinson (Lawrence, KS), Burt L. Monroe, Jr. (Louisville, KY). Wilbur B. Quay (New Bloomfield, MO), Gus Swanson (Ft. Collins, CO), Tom Tacha (Kingsville, TX), Frederick R. Wells, II (Reynoldsburg, OH). The secretary was informed later of the following members who had died since this list was compiled: John Aldrich (Tucson, AZ) and Katherine A. Goodpasture (Nashville, TN).

The treasurer's report was then presented by Doris Watt.

The editor's report was offered by Charles Blem.

William (Ted) Davis, chair, presented the report of the nominating committee (Mary Clench and Jerome A. Jackson members): President, Keith L. Bildstein; First Vice-president, Edward H. Burtt, Jr.; Second Vice-president, John C. Kricher; Secretary, John A. Smallwood; Treasurer, Doris J. Watt; Members of the Council, 1996–1998, Margaret C. Brittingham and Herbert T. Hendrickson.

Mary Clench moved for adjournment and George Hall seconded the motion, and the meeting was adjourned at 08:58.

SECOND BUSINESS MEETING

The second business meeting was called to order by President Conner at 11:03 on Saturday, 6 May, in the Jefferson Davis Amphitheater.

The Auditing Committee's report was presented by Judy McIntrye (with Fred Lohrer) and indicated the spread sheet and treasurer's report totals were found to balance and that the books were quite in order.

The President recalled the report of the nominating committee to the floor, asking for any additional nominations. Since none were immediately forthcoming, Jerry Jackson moved and Phillips Street seconded that the nominations be closed and further, that the secretary cast a unanimous ballot for the nominees for all offices. The motion passed and the secretary did as directed.

Sandra Gaunt gave a report for the Ornithological Council, our representatives, Dan Petit and Larry Jahn, not being present at this session. She reviewed the increasing presence of the Council on the Washington scene and noted that Bette Ann Schreiber has been hired as a part-time Director.

REPORT OF THE RESOLUTIONS COMMITTEE

Erica Noll presented the report of the committee:

RESOLUTION ON THE ENDANGERED SPECIES ACT

WHEREAS the global rate of species loss is probably greater today than at any other time in the earth's history; and

WHEREAS the most important causes of extinction today are habitat loss and overexploitation; and

WHEREAS over its 22-year history the Endangered Species Act of 1973 has proven to

be one of the most important environmental laws in the United States in that it provides a flexible framework for protecting endangered species and their habitat; and

WHEREAS in the Endangered Species Act Congress has declared that "various species of fish, wildlife, and plants in the United States have been rendered extinct as a consequence of economic growth and development untempered by adequate concern and conservation;" and

WHEREAS the Endangered Species Act is currently up for reauthorization; and

WHEREAS strong attacks have been made against the Endangered Species Act arguing that economic interests should come before the needs of endangered species; and

WHEREAS these attacks often include exaggerated claims of economic loss, losses to personal property, and present negative and erroneous characterizations of endangered species;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society encourages the Congress of the United States to reauthorize the Endangered Species Act with species welfare as the central focus and sound biology as the dominant criterion for decision making so that it can continue to serve as a model to the rest of the world for legislation that recognizes the significance of ecosystems and protects endangered and threatened species and their ecosystems from adverse impacts of human actions; and

BE IT FURTHER RESOLVED that the Wilson Ornithological Society urges ornithologists, and local, regional and national bird clubs and ornithological organizations to actively support reauthorization and strengthening of the Endangered Species Act by providing informed opinions and relevant data to those influencing and making our laws; and

BE IT FURTHER RESOLVED that the Wilson Ornithological Society exhorts the Secretary of the Interior and the Secretary of Commerce, the Secretaries mandated by the Endangered Species Act to implement its provisions, to implement stronger public education programs relative to the Endangered Species Act, its implementation, and species protected under it, and to swiftly, strongly, and consistently provide public rebuttal to disinformation made public concerning the Endangered Species Act and the species it protects.

The motion to accept this resolution was made by Herb Hendrickson, seconded by Jed Burtt, and passed.

RESOLUTION ON THE LOCATION OF CASINOS IN AQUATIC AND ESTUARINE ENVIRONMENTS

WHEREAS aquatic and estuarine ecosystems are ecologically highly productive and essential as nursery areas for commercial fisheries and shell fisheries as well as a high diversity of non-commercial species; and

WHEREAS these interfaces between land and water along the northern Gulf of Mexico are of paramount importance as landfall and departure areas for Neotropical migrant landbirds, essential wintering areas for thousands of shorebirds, including the endangered Piping Plover, and include significant nesting and feeding areas for already troubled Least Terns and Snowy Plovers, Seaside Sparrows, and other birds; and

WHEREAS such ecosystems are already globally stressed as a result of human development and recreational activities in and near them and as a result of chemical runoff from roads and agricultural and industrial areas; and

WHEREAS many states now have or are considering legalized gambling in the form of casino operations; and

WHEREAS many states have limited casino development to sites that are on water; and

WHEREAS construction and operation of casinos in shallow water areas further limits the area available for the natural functioning of the ecosystems and further contaminates

these ecosystems as a result of runoff from roads and parking areas, and decreases primary productivity as a result of increased turbulence, deposition of sediments, and shading;

THEREFORE BE IT RESOLVED THAT The Wilson Ornithological Society urges states to reconsider the requirement that casinos be constructed and operated in these sensitive environments; and

BE IT FURTHER RESOLVED THAT The Wilson Ornithological Society urges that states with casinos in such sites institute close ecological monitoring to quantify the effects of such human developments on the functioning of the natural ecosystems; and

BE IT FURTHER RESOLVED THAT The Wilson Ornithological Society urges states to take decisive action to limit negative environmental impacts of casino development and to correct continuing degradation of these aquatic and estuarine ecosystems; and

BE IT FURTHER RESOLVED THAT The Wilson Ornithological Society urges that operators of existing casinos recognize the sensitivity of the environment in which they are operating and take steps to protect that environment and to educate their patrons as to the ecological and economic importance of that environment.

The motion to accept this resolution was made by Dick Stiehl and seconded by Jed Burtt and passed.

RESOLUTION CONCERNING THE RED-COCKADED WOODPECKER IN KENTUCKY

WHEREAS the Red-cockaded Woodpecker is an endangered species endemic to the mature pine forests of the southeastern United States; and

WHEREAS the northernmost population of the Red-cockaded Woodpecker is now found only on the Daniel Boone National Forest on the Cumberland Plateau of south-central Kentucky; and

WHEREAS the Red-cockaded Woodpecker population of the Cumberland Plateau has been isolated from other populations for many decades and has adapted to this specific habitat at least to the extent that individuals from this population are significantly larger than individuals from other populations and they make a greater use of hardwood vegetation as foraging sites; and

WHEREAS this population has been reduced to approximately six known individuals, a precipitous decline following intensive management activity; and

WHEREAS the natural pine habitats of the Cumberland Plateau occur as linear strips along ridges; and

WHEREAS these habitats include pine species not found in most of the coastal plain of the southeastern United States; and

WHEREAS these pine habitats are the products of fire regimes, climate, and topography that differ substantially from those pine habitats of the remainder of the southeastern United States;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society strongly urges the U.S. Fish and Wildlife Service and the U.S. Forest Service: (1) to conduct thorough surveys of all habitat to ascertain the presence or absence of additional birds; (2) to use ecologically appropriate management for the Cumberland Plateau to restore natural old growth systems; (3) to minimize or preclude disturbance and handling of birds, particularly to preclude climbing of nest trees and banding of nestlings until the population has recovered to a less critical level and then only when needed information can be obtained in no other way; (4) to minimize or preclude the translocation of birds from other populations onto the Daniel Boone National Forest because of a) the unique nature of the native population and its habitat; b) the fact that much of the Daniel Boone National Forest has not been system-

atically searched for Red-cockaded Woodpeckers; and c) because of the potential for introduction of parasites and/or disease to this critically small population.

The motion to accept this resolution was made by Richard Banks, seconded by Herb Hendrickson and passed.

RESOLUTION TO PROTECT HABITAT AROUND DYKE MARSH, ALEXANDRIA, VIRGINIA

WHEREAS Dyke Marsh is a significant wetland area near the nation's capital and as such is an important symbol of the nation's commitment to natural areas; and

WHEREAS Dyke Marsh has been used for the education and enjoyment of local residents; and

WHEREAS one of the options being considered by the Woodrow Wilson Bridge Improvement Study's Coordinating Committee for an expanded crossing of the Potamac River is a high bridge along a "southern alignment"; and

WHEREAS such an alignment would do severe environmental damage to the sensitive Hunting Creek–Hunting Bay–Dyke Marsh ecosystem, including destruction of extensive wetlands that play a crucial role in preserving air and water quality and habitats of flora and fauna; and

WHEREAS construction of a river crossing through this ecosystem, which has been rendered particularly fragile by previous filling, dumping and other degredations, would do irreparable harm to this valuable natural resource; and

WHEREAS recreational opportunities along this stretch of river would be precluded or hampered by a bridge that would also block vistas of the river and parklands from the George Washington Memorial Parkway;

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society urges the Woodrow Wilson Bridge Improvement Study Coordinating Committee to drop the "southern alignment" as an option to be considered, and

BE IT FURTHER RESOLVED that in any plan to construct an expanded river crossing along the current alignment care be taken to ensure that remaining wetlands along Cameron Run, Virginia not be destroyed or degraded.

The motion to accept this resolution was made by Richard Banks and seconded by Ted Davis. It passed.

COMMENDATION

WHEREAS the Wilson Ornithological Society and the Virginia Society of Ornithology held a joint meeting in Williamsburg, Virginia at the invitation of the the Virginia Society of Ornithology, Williamsburg Bird Club, and the College of William and Mary; and

RECOGNIZING that the Committee on Local Arrangments, under the sound direction of Ruth A. Beck, provided us with a diverse and entertaining array of exhibits, special events, field trips and evening social events; and

RECOGNIZING that the Committee on the Scientific Program under the equally capable direction of Edward H. Burtt, Jr. arranged outstanding scientific lecture sessions and poster sessions, including a special symposium on "Ornithology in northern Central America;" and

WHEREAS all who have attended this meeting have enjoyed and been educated by it,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commend the Commitee on Local Arrangements, the Committee on the Scientific Program, and local sponsors for their efforts toward this enlightening meeting in historic Williamsburg.

The acceptance of this resolution followed a motion by Paul Hamel that was seconded by Mary Clench and the vote of members present with great acclaim.

President Conner introduced the following resolution:

WHEREAS John L. Zimmerman has served the Wilson Ornithological Society long, well, and faithfully as its Secretary; and

WHEREAS the Society has greatly benefitted from his careful attention to its affairs for eleven years; and

WHEREAS he has often discharged his duties with lightening speed (what other ornithological society has the minutes of its annual Council meeting written before the Secretary arrives back home?); and

WHEREAS John's regard for, and his continued willingness to contribute toward the welfare, of the Society has led to an extraordinarily generous invitation to host the 78th meeting;

THEREFORE BE IT RESOLVED that the Officers, Council, and Membership of the Wilson Ornithological Society extend their heartfelt gratitude to John Zimmerman for his many years of service as Secretary, and look forward to enjoying the 1997 meeting in Manhattan under his able leadership.

This motion to accept this resolution was made by Clait Braun and seconded by Mary Clench and passed with applause by the membership.

Mary Clench then moved the meeting be adjourned. And after a second by Ted Davis, it was.

REPORT OF THE TREASURER
1 July 1994 to 31 June 1995

GENERAL FUNDS

Balance Forward		$ 82,520.43
Receipts		
Regular and Sustaining Memberships	$ 31,190.00	
Student Memberships	4,433.00	
Family Memberships	150.00	
Total Dues		$ 35,773.00
Subscriptions	$ 24,782.00	
Back Issues	446.50	
Newsletter Subscriptions	254.70	
Contributions from Authors for Page Charges	9,280.00	
Total Income from the Publications		$ 34,763.20
Contributions to The Van Tyne Library	$ 255.00	
Contributions to the Student Membership Endowment		
Contributions to the Wilson Award Endowment		
Contributions to the General Endowment (Life, Patrons)	2,125.00	
Contributions to the Research Fund		
Contributions to the General Endowment	563.00	
Unrestricted Contributions	413.00	
Total Contributions		$ 3,356.00
Royalties		832.83
Interest from Endowments		20,923.14
Interest from Checking Account		900.94

Dividends from Dreyfus Account (reinvested)		931.64
List Rental		550.00
Refund from Joint Meeting		4,050.20
Miscellaneous		257.50
TOTAL RECEIPTS		$102,338.45
Disbursements		
Bulletin Publication		
June 1994	$ 19,311.57	
September 1994	14,938.68	
Reprint of March 1994	3,472.25	
December 1994	19,762.67	
March 1995	18,989.12	
Editor's expenses	5,339.31	
Total Publication Costs		$ 81,813.60
OSNA Expenses	$ 11,389.00	
President's expenses	0.00	
Secretary's expenses	62.16	
Treasurer's expenses	411.91	
Treasurer's bond	106.00	
Meeting advance	249.21	
Editor's travel expenses	0.00	
Incorporation fee	5.00	
Awards Committee	138.88	
Printing, storage and mailing of back issues	172.30	
Advertisement (Allen Press)	0.00	
Program Committee	246.16	
Van Tyne Library	0.00	
AAZN Dues	100.00	
Total Operating Expenses		$ 12,880.62
Organizational Awards	$ 3,250.00	
ICBP Contribution		
Total Philanthropies		$ 3,250.00
TOTAL DISBURSEMENTS		$ 97,944.22
Ending Balance		$ 86,914.66

CASH ACCOUNTS

First Source Bank Checking Account 1 May 1995	$ 58,558.02	
Dryfus Liquid Assets 31 March 1995	$ 28,205.33	
Editor's Account	168.29	
Total Cash on Hand		$ 86,931.64
Van Tyne Library Accounts Starting Balance	$ 2,256.17	
Receipts	$ 1,754.18	
Expenses	1,484.56	
Ending Balance		$ 2,525.79

DESIGNATED ACCOUNTS

Stewart Award (Endowment Principal $22,879.69)

1994 Balance	$	63.41
1994 Earnings[1]	$	894.78
Funds Disbursed for Awards		1,200.00
Balance		−241.81
Sutton Color Plate Fund (Endowment Principal $55,227.79)		
1994 Balance	$	525.81
1994 Earnings[1]	$	2,174.39
Funds Disbursed for Color Plates 1994–95		2,200.00
1995 Balance		500.20

TOTAL ENDOWMENT FUNDS

1989 Market Value	$386,992.00
1990 Market Value	$372,063.00
1991 Market Value	$423,698.00
1992 Market Value	$430,258.00
1993 Market Value	$487,786.00
1994 Market Value	$425,155.00
1995 Market Value (March 95)	$463,530.00

[1] Based on 3.9% interest on Mellon account.

EDITOR'S REPORT—1994

In 1994, 180 manuscripts (99 major papers, 81 short communications) were received by *The Wilson Bulletin* editorial office. This is 5 less than in 1993. Of these, 39% were accepted and 61% were rejected. The time between receipt of manuscript from the author(s) and our return of the manuscript with referee comments nearly always has been less than three months. No manuscript required more than four months for a decision. There is a small backlog of manuscripts, but accepted revisions almost always have been published in the next scheduled issue. Frontispiece articles take a bit longer. The average time between receipt of a manuscript and its appearance in *The Wilson Bulletin* in 1994 was almost always less than a year. A few papers required longer because authors were slow to return revisions.

I am grateful to the editorial board—Kathy G. Beal, R. N. Conner, and J. A. Smallwood—for their timely, skilled evaluations of many of the manuscripts submitted to the journal. I also thank George A. Hall for his editorship of the book reviews section. George resigned this position effective with the September, 1995 issue, and the new review editor is William E. Davis, Jr. Assistant Editors Leann Blem and Albert E. Conway are responsible for the consistency of style and format, and for making arcane prose more readable. I thank them for their efforts. Kathy G. Beal deserves special praise for continuing to assemble the index for *The Wilson Bulletin.* This a tedious task and the entire society benefits from her careful work. For seven years Leann Blem has provided much of the manual labor that keeps the editorial office running and she catches many of the small errors that can plague a publication. As always, I remain open to suggestions as to how to improve the service we provide the readers and authors, and invite you to make your opinions known to me.

C. R. Blem, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE—1994

The end of another year's activity seems to have taken us a bit by suprise. The undersigned chairman, not helped by a brief hospital stay last summer followed by some months of slow recuperation, has hardly performed as was to be expected. As usual, however, Janet Hinshaw and her helpers have managed all the business of the WOS Library along with that of the the Bird Division Library in the University of Michigan Museum of Zoology, where our large collections are well housed and available for use. Thanks especially to Pat Ahrens, Bird Division secretary, for her help. Things have continued to move forward normally, as the facts and figures show.

Gifts were distributed as follows: 1 monograph to Manomet Bird Observatory, 1 monograph to UNAM (Mexico), 12 journal issues to Walter Thiede, 107 journal issues to Hudsonia Institute, 1 book to Universite' d'Antananarivo in Madagascar, 12 journal issues to University of Texas-Pan American, 10 journal issues to Albion College (Michigan), 78 issues to the University of Kansas, 4 issues to P. Meininger, and 196 issues to Station Ornithologique Suisse. There are about 10 of these outgoing collections in all.

Donations to the library were from 20 members and institutions: Absearch, R. Bayer, A. Berger, M. Clench, S. Conant, Edward Grey Institute, George Hall (review copies), J. Hinshaw, J. Huber, P. Meininger, M. McNicholl, K. Parkes, R. Payne, R. Pettit, J. Spendelow, Station Ornithologique Suisse, C. Strahler, Welder Wildlife Foundation, J. Wiley, and M. D. Williams. These included 25 books and monographs, 355 reprints, 6 reports, 633 journal issues, and 1 computer data base.

During the year, 55 separate loans were made to 33 people. In all, there were 169 photocopied articles, 3 reprints, 22 books, and 4 journals lent.

Exchanges from 122 institutions provided 155 journals, books, and reprints. From 27 individuals and institutions we received 32 publications as gifts. From 21 subscriptions we received 29 journals.

Sales of 85 duplicate books netted $1940 for the New Book Fund; 12 books were purchased from the fund for $310.35, along with $860.50 worth of journal subscriptions and back issues.

It is good to see more and more activity of this sort, which demonstrates how surplus items can be turned into substantial funds to augment our current holdings.

Our heartfelt thanks go out to all the members who have made contributions, and we encourage ever more of them to do so, and to make use of the loan opportunities we offer.

William A. Lunk, *Chair*

REPORT OF THE CONSERVATION COMMITTEE

The Conservation committee has incorporated its concerns into the resolutions voted upon during the annual meeting and has no other written report.

Jerome A. Jackson, *Chair*

REPORT OF THE MEMBERSHIP COMMITTEE

Four WOS members currently serve on the membership committee: Jim Ingold at Louisiana State University, Mark Woodrey at the Mississippi Museum of Natural Science, Dave Cimprich at the University of Southern Mississippi, and myself at Montclair State University in New Jersey.

This past year I received about 18 letters from people interested in joining WOS. My established protocol is to send to each a membership brochure and a personal letter welcoming them to the Society. About half of these new members include their dues with their letter; for these I complete an application which I forward with their check to the OSNA business office, in addition to sending them a welcome letter and brochure. I also received several inquiries about institutional subscriptions (e.g., new subscribers, changes of address), which I forwarded to OSNA.

The other members of the committee have been active in their respective niches: Mark Woodrey sends membership invitations to authors who publish in *The Wilson Bulletin,* Jim Ingold contacts nonmembers who make presentations at the annual meetings, and Dave Cimprich oversees the itinerary of the membership poster. In addition to the joint WOS/AOU/COS meeting in Missoula, the poster was also displayed at the joint AFO/Federation of New York State Bird Clubs meeting in Rosendale, New York.

The membership committee would welcome the participation of any new committee members who are interested in contributing to the ongoing membership functions, or introducing new membership strategies.

As the supply of membership brochures has dwindled to a few dozen, it is time to print more. Please send any suggested revisions to me at your earliest convenience. I think it is noteworthy that the same dues structure, as outlined in the brochure, has been in effect since I joined the membership committee in 1990. Thus, with respect to a modest national inflation rate and the continually increasing value of *The Wilson Bulletin* and the other WOS products, membership in the WOS has been characterized by a steady increase in the percent return on member investment.

John A. Smallwood, *Chair*

The Committee on Scientific Program, chaired by Edward H. Burtt, Jr. with Richard Bradley and Oliver Komar, presented the following program assisted by session moderators Jon C. Barlow, Richard P. Gerhardt, Carola A. Haas, Paul B. Hamel, John C. Kilgo, Chandler S. Robbins, and Richard H. Yahner.

PAPERS SESSIONS

Richard H. Yahner and Carolyn G. Mahan, School of Forest Resources, Penn. State Univ., "Depredation of artificial nests in a managed forest"

Charles R. Blem, Leann B. Blem, and Lesa F. Steele, Dept. Biol., Virginia Commonwealth Univ., "Clutch size of Prothonotary Warblers in Virginia"

Robert A. Sargent, John C. Kilgo., Brian R. Chapman, and Karl V. Miller, Warnell School of Forest Resources, Univ. Georgia, "Nest success of Kentucky Warbler and Hooded Warbler in southeastern bottomland forests"

Amy L. Meehan, Dept. Fish. and Wildl. Sci., Virginia Polytech. Inst. and State Univ., "Low reproductive success of a Neotropical migrant songbird in an extensively forested landscape"

Jameson F. Chase, Dept. EPO Biol., Univ. Colorado, "Cowbird parasitism and nest predation on Solitary Vireo nests: does nest choice make a difference?"

J. Edward Gates and Daniel R. Evans, Appalachian Environ. Lab., Center Environ. and Estuarine Studies, Univ. Maryland, "Cowbird spatial ecology on anthropogenic rorest landscapes"

Richard P. Gerhardt and Dawn M. Gerhardt, Peregrine Fund, and Miguel Angel Vasquez, El Parque Nacional Tikal, Guatemala, "Breeding biology, food habits, and siblicide of Swallow-tailed Kites in northern Guatemala.

A. Townsend Peterson, Mus. Nat. Hist., Univ. Kansas, and Oliver Komar, Dept. Zool., Ohio Wesleyan Univ, "Non-breeding distribution of the Cave Swallow (*Hirundo fulva*)"

Oliver Komar, Dept. Zool., Ohio Wesleyan Univ., "Communal roosting behavior of the Cave Swallow (*Hirundo fulva*)"

Donald H. Messersmith, Dept. Entomol., Univ. Maryland, "Bird survey of Blue Creek Area, southern Belize"

C. S. Robbins, B. A. Dowell, and J. E. Fallon, National Biol. Serv., Patuxent Wildl. Res Cent., "Banding and point count studies in Guatemala"

Dwight Peake, Galveston, TX, Giulietta Fargion, Marine Biol., Texas A&M, Keith Mullin, SE Fish. Sci. Cent., Robert Pittman, SW Fish. Sci. Cent., and Robert Benson, Texas A&M, "Seabirds of the northwestern and central Gulf of Mexico"

R. Michael Erwin, J. G. Haig, D. B. Stotts, and J. S. Hatfield, Patuxent Environ. Sci. Cent., "Dispersal; in juvenile wading birds from a Virginia colony"

Bryan D. Watts, Cent. Conserv. Biol., College William & Mary, "Influence of patch size on incidence rates and community organization in marsh birds"

Crystal Matthews, Biol. Dept., College William & Mary, "Effects of substrate on hatching success in Black Skimmers at the Hampton Roads Bridge-Tunnel, Hampton, Virginia"

Amanda Allen, Cent. Conserv. Biol., College William & Mary, "Tidepool value as foraging patches for breeding and migrating birds in tidal salt marshes in the lower Chesapeake Bay"

W. Herbert Wilson, Dept. Biol., Colby College, "Foraging behavior of Semipalmated Sandpipers in the Bay of Fundy; stereotyped or prey sensitive?

John C. Kilgo, Robert A. Sargent, Karl V. Miller, and Brian R. Chapman, Warnell School of Forest Resources, Univ. Georgia, "Hooded Warbler nest-site selection in southeastern bottomland hardwoods"

Bradley D. Ross and Richard H. Yahner, School Forest Resources, Penn. State Univ., "Wood Thrush distribution and nesting success in a managed forest in central Pennsylvania"

Paul B. Hamel, USDAFS, Southern Hardwoods Lab., "Spatial distribution of breeding canopy warblers in the Mississippi alluvial valley"

Paul Bedell, Richmond, VA, "Evidence of dual breeding ranges for the Sedge Wren in the central Great Plains"

E. Dale Kennedy and Douglas W. White, Biol. Dept., Albion College, "Nest vandalism by House Wrens affects the breeding success of Bewick's Wrens"

Clait E. Braun, Colorado Div. Wild., and Jessica R. Young, Dept. Biol., Hampden-Sydney College, "A new species of Sage Grouse from Colorado"

Jon C. Barlow and James A. Dick, Dept. Ornithol., Royal Ont. Mus., "Speciation in meadowlarks in Texas"

Ernest J. Willoughby, Dept. Biol., St. Mary's College of Maryland, "Geographic variation of molt in the Lesser Goldfinch, *Carduelis psalria*"

John A. Smallwood, Dept. Biol., Montclair State Univ., Michael P. Moulton, Dept. Wildl. Ecol. and Conserv., Univ. Florida, and Denson K. McLain, Biol. Dept., Georgia Southern Univ., "Dichromatism in the genus *Falco:* sexual selection versus an adaptive peak"

Daniel R. Ardia, Dept. Environ. and Forest Biol., SUNY-Syracuse, "An experimental investigation of gender related differences in habitat use in American Kestrels"

Thomas S. Risch, Savannah River Ecol. Lab., "Effects of parental quality and egg size on Herring Gull chick performance"

John N. Mager, David R. Osborne, Dept. Zool., Miami Univ. (OH), and David C. Evers, Dept. Fish. & Wildl., Univ. Minnesota, "Parental effort in the seasonally monogamous Common Loon (*Gavia immer*)"

Briony Roberts, Dept. Biol., Virginia Polytech. Instit. and State Univ., "Vocal behavior of the Puerto Rican Parrot (*Amazona vitatta*) and its applicability to individual recognition"

Douglas W. White and E. Dale Kennedy, Biol. Dept., Albion College, "Avian fruit choices in paired-comparison field trials"

John L. Zimmerman, Div. Biol., Kansas State Univ., "Impact of grazing on the tallgrass prairie breeding bird community"

Amy R. Lewis and Richard H. Yahner, School Forest Resources, Penn. State Univ., "The effects of forest management on the abundance and distribution of Rufous-sided Towhees"

John B. Dunning, Jr., Dept. Forestry and Nat. Resources, Purdue Univ., "Managment impacts on a non-target species: Bachman's Sparrow in a Red-cockaded Woodpecker forest"

Richard N. Conner and D. Craig Rudolph, Southern Forest Res. Sta., USFS, "Southern pine beetle induced mortality of natural and artificial Red-cockaded Woodpecker cavity trees"

Lisa Billow, Dept. Biol., West Chester Univ. (PA), "An analysis of change in land use and bird populations on breeding-bird survey routes in the Delaware Valley from 1970 to 1990"

Carola A. Haas, Dept. Fish. & Wildl. Sci., Virginia Polytech. Instit. and State Univ., "Ten-year trend in a breeding population of Loggerhead Shrikes (*Lanius ludovicianus*) in North Dakota"

Gregory S. Keller, Richard H. Yahner, and Ronald W. Rohrbaugh, Jr., School Forest Resources, Penn. State Univ., Gerald L. Storm, Penn. Coop. Fish and Wild. Res. Unit, and John Karish, National Park Serv., "Monitoring protocols at Gettysburg National Military Park"

Bradley D. Ross, Richard H. Yahner, and Gary Petersen, School Forest Resources, Penn. State Univ., and Jerry Hassinger, Penn. Game Comm., "Correlating habitat and bird variables using classified land uses and extensive wildlife data sets"

Maria Jose Gonzalez, Guatemala City, "The Ocellated Turkey, its habitat use and reproductive ecology"

Oliver Kornar, Dept. Zool., Ohio Wesleyan Univ., "Avian biodiversity in El Salvador"

Bruce Miller, Wild. Conserv. Soc., "Known birds of Belize, a review of distributions and selected habitat associations"

Maria de Lourdes Avila Hernandez, Instit. de Hist. Nat. Chiapas, "The Quetzal (*Pharomachrus mocinno mocinno*) and its conservation in the Mexican southeast"

A. Townsend Peterson, Mus. Nat. Hist., Univ. Kansas, "Documenting avian diversity in Central America: research challenges and conservation implications"

POSTERS

Jeffrey J. Buler, St. Mary's College of Maryland and Randall Dettmers, Ohio Coop. Wildl. Res. Unit, "Effect of host nest cover and distance to forest edge on Brown-headed Cowbird (*Molothrus ater*) parasitism"

Michael Carey, Dept. Biol. Univ. Scranton, "Effects of age and settlement date on extra-pair mating in Field Sparrows"

Jameson F. Chace, Dept. EPO Biol., Univ. Colorado, "Nest-site selection by Solitary Vireos"

Richard P. Gerhardt, Dawn M. Gerhardt, and Craig J. Flatten, The Peregrine Fund, and Normandy Bonilla, El Parque Nacional Tikal, Guatemala, "Food habits, home range, and breeding of two sympatric *Ciccaba* owls"

H. T. Hendrickson, Dept. Biol., Univ. North Carolina-Greensboro, "Further negative correlation in wintering population sizes of introduced House Finches and native Purple Finches - the New York City area"

Michael J. Justice and Teresa C. Justice, Dept. Pysch., Univ. North Carolina-Greensboro, "Evidence that a coverable badge is sexually selected by female mockingbirds"

C. S. Robbins, B. A. Dowell, J. Fallon, National Biol. Serv., Patuxent Wild. Res. Cent. and J. Hepinstall, Univ. Maine, "Predicting population declines from habitat change in Belize"

Richard C. Banks and G. "Chuck" Banks, National Biol. Serv., U.S. Natl. Mus. Nat. Hist., "Variation in wintering Old World White-fronted Geese"

1995 NABS RESEARCH AWARDS

The North American Bluebird Society is pleased to announce the results of its eleventh annual research grant's program. The following individuals are recipients of the 1995 research awards:

BLUEBIRD GRANTS

Laura R. Lee, University of Illinois. Environmental Effects of the Reproductive Ecology of the Eastern Bluebird

Michael H. Kesner, Indiana University of Pennsylvania. Influence of Prior Box Occupancy by White-footed Mice and Subsequent Parasitism of Nesting Eastern Bluebirds on Nesting Success

STUDENT GRANTS

Paul E. Allen, Cornell University. A Baseline Population Estimate and Feasibility of Nest boxes as a Conservation Tool for the Bahama Swallow

Susan M. Hitchcox, University of Montana. A Comparison of Abundance and Nest Success of Cavity-nesting Birds in Salvaged Logged and Uncut Patches Within a Burned Forest

GENERAL GRANTS

Richard L. Bonar, Foothills Forest, Alberta. Pileated Woodpecker Habitat Ecology in Boreal Forests

Wilson Bull., 107(4), 1995, pp. 790–813

INDEX TO VOLUME 107, 1995

By Kathleen G. Beal

This index includes references to genera, species, authors, and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text. Common names are as they appear in the volume unless otherwise specified. Reference is made to books reviewed, and announcements as they appear in the volume.

abundance
  of Columba squamosa after Hurricane Hugo, 727–733
  of Myiopsitta monachus in Chicago, 510–517
  of Neotropical migrants in Jamaica, 577–589
  of overwintering passerines in hardwood forests, 698–708
  of raptors in Puerto Rico, 452–462
Accipiter cooperii, 720
  gentilis, 720
  sp., 536
  spp., 100, 553
  striatus, 452–462, 544, 566
Aceros spp., 103
Actitis macularia, 286
activity budget
  of pre-nesting Grus canadensis in arctic Canada, 752–756
adaptive advantage
  of delayed plumage maturation in female Tachycineta bicolor, 153–164
Aegolius acadicus, 21, 721
  ridgwayi, 21
Aegotheles spp., 95
Aeronautes spp., 103
Agelaius phoeniceus, 127, 129, 165, 378, 479, 540, 709–718
Aimophila ruficeps, 721
Ainley, Marianne G., Restless energy, a biography of William Rowan, reviewed, 185–186
Aix sponsa, 108
Akodon sp., 679
Alauda gulgula, 97
  spp., 103
Albatross, Laysan, see Diomedea immutabilis
Alca torda, 397–412
  spp., 102
Alectoris spp., 111
Alectura spp., 101
Alopex lagopus, 397–412 (Frontispiece)
Alopochen aegyptiacus, 108
Amadon, Dean, review by, 773
Amaurornis spp., 101
Amazona leucocephala bahamensis, 526
  spp., 165
  vittata, 518–529
Ammodramus bairdii, 709–718
  savannarum, 709–718
  spp., 248
Amphispiza bilineata, 650
Anas acuta, 239, 363
  americana, 354, 363
  clypeata, 108
  crecca, 262
  cyanoptera, 64–72, 262
  discors, 69
  fulvigula maculosa, 548–551
  platyrhynchos, 55–63, 69, 107, 262, 354, 355, 359–365, 548–551
  rubripes, 548–551
  spp., 93, 100, 261
  strepera, 70, 108, 353, 363
Anastomus spp., 100
anatomy
  of avian cecum, 93–121
Anderson, Bruce H., see Stevenson, Henry M., and ———
Anhima spp., 95, 100
Anhinga spp., 100
Anianiau, see Hemignathus parvus
Anolis app., 566
Anous spp., 102
Anser albifrons, 246, 752–756
Anseranas spp., 100, 217

ant, red imported fire, see Solenopsis invicta
Anthony, Robert G., see Marr, N. Vern, W. Daniel Edge, ———, and Ray Valbur
Anthus rubescens, 180
Anumbius annumbi, 734–738
Apanius, Victor, see Seutin, Gilles, and ———
Aphelocoma coerulescens, 44, 127, 129, 721
  coerulescens coerulescens, 41, 50
  ultramarina, 721
Aptenodytes patagonicus, 323
  spp., 98
Apteryx spp., 98
Apus spp., 103
Aquila chrysaetos, 256, 271, 682, 683
Ara spp., 102
Aramides spp., 101
Aramus spp., 101
Archilochus alexandri, 721
  colubris, 194, 566
Ardea herodias, 434, 446
  spp., 100
Ardeola spp., 100
Arenaria interpres, 432
Argusianus spp., 101
artwork
  of students of Alexander Wilson, 193–213
Asch, Andreas, and Daniel D. Roby, Some factors affecting precision of the total body electrical conductivity technique for measuring body composition in live birds, 306–316
Asio flammeus, 452, 455, 765
  spp., 103
Astrapia nigra, 372
Athene brama, 97
  noctua, 14
  spp., 103
Avocet, Red-necked, see Recurvirostra novaehollandiae
Aythya affinis, 108, 354
  americana, 108, 338–358
  collaris, 108, 354
  marila, 108, 353, 363
  spp., 108
  valisineria, 108, 346, 351, 338–358
Baldassarre, Guy A., see Losito, Michael P., and ———
Bananaquit, see Coereba flaveola
Bartella, Mónica B., see Navarro, Joaquín L., ———, and Enrique H. Bucher
Bartramia longicauda, 709–718
bass, see Micropterus spp.
  smallmouth, see Micropterus dolomieui
  yellow, see Morone mississippiensis
Bassariscus astutus, 262
Bawa, Jamaljit, see McDade, Lucinda A., ———, Henry A. Hespendheide, and Gary S. Hartshorn
Beardsell, C. M., see Emison, W. B., ———, and I. D. Temby
beaver, see Castor canadensis
behavior
  aggressive
    in Larus delawarensis due to investigator disturbance, 140–152
  breeding
    calls of Lagopus lagopus, 496–509
    nesting of Amazona vittata, 518–529
  copulation
    food delivery and food holding in Lanius ludovicianus, 762–764
  feeding
    effect on insect community structure, 746–752
    kleptoparasitism of Lophodytes cucullatus by Larus delawarensis, 379–382
    of breeding Anas cyanoptera, 64–72
    of breeding Haliaeetus leucocephalus, 258–274
    of Haematopus longirostris and Haematopus fuliginosus, 629–640
    of Haliaeetus leucocephalus on Ovis aries carcasses, 251–257
    predator-prey relationship between Charadrius wilsonia and Uca cumulanta, 73–80
  flocking
    effect of food supplementation and predator simulation on mixed species, 542–547
  foraging
    sociability of nesting wading birds, 437–451
    within-season trends in Parus gambeli, 655–666
  mate guarding
    tactics in Myiarchus crinitus, 757–761

philopatry
record in Grus canadensis tabida, 766
roosting
of Vermivora citrea in non-breeding season, 374–376
Beidleman, Richard G., review by, 185–186
Bell, Ross, see Heinrich, Bernd, and ———
Bellrose, Frank C., and Daniel J. Holm, Ecology and management of the Wood Duck, reviewed, 569–571
Benkman, Craig W., see Hill, Geoffrey E., and ———
bias
in Christmas Bird Counts for feeder species, 122–130
Bildstein, Keith L., review by, 770–771
Bildstein, Keith L., White Ibis: wetland wanderer, reviewed, 190
bird of paradise, see Ptiloris sp. and Parotia sp.
Bird of Paradise, Standardwing, see Semioptera wallacii
Birkhead, T. R., and D. N. Nettleship, Arctic fox influence on a seabird community in Labrador: a natural experiment, 397–412
Biziura lobata, 214–234
Blackbird, Brewer's, see Euphagus cyanocephalus
Red-winged, see Agelaius phoeniceus
Yellow-headed, see Xanthocephalus xanthocephalus
Blackwell, Rachelle C., see Dodge, Anthony G., Adam J. Fry, ———, and Robert M. Zink
Blem, Charles R., reviews by, 189–190, 192, 572–573, 573, 574
Bluebird, Eastern, see Sialia sialis
Western, see Sialia mexicana
boa, Puerto Rican, see Epicrates inornatus
Bobolink, see Dolichonyx oryzivorus
Bobwhite, Crested, see Colinus cristatus
Northern, see Colinus virginianus
body fat
use of total body electrical conductivity technique, 306–316
body mass
of migrating Calidris minutilla in British Columbia, 413–422
seasonal and diurnal variation in Parus atricapillus and Zonotrichia albicollis, 723–727
Bolen, Eric G., and Dan Flores, The Mississippi Kite, reviewed, 188–198
Bollinger, Eric K., see Linder, Eric T., and ———
Bombycilla cedrorum, 125, 127, 129, 165, 701, 702
garrulus, 125, 127, 129
Bonasa umbellus, 738
Bos taurus, 262
botfly, see Philornis pici and Philornis seguyi
Boyd, Hugh, see Fox, Anthony D., ———, and Robert G. Bromley
Brachyramphus brevirostris, 235–250
marmoratus, 178–179, 235–250
Bradshaw, Dana S., see Watts, Bryan D., and ———
Brant, see Branta bernicla
Branta bernicla, 246
canadensis, 112, 246, 432, 752–756
breeding
biology
effect of exogenous testosterone on Mimus polyglottos, 538–542
of Charadrius alexandrinus at Great Salt Lake, Utah, 275–288
of Dendroica discolor paludicola and Dendroica petechia gundlachi, 475–484
of Geranoaetus milanoleucus in Patagonia, 675–685
of Myiopsitta monachus in Chicago, 510–517
success
of communally nesting Myiopsitta monachus, 742–746
of Sterna hirundo on navigational aids and natural islands, 423–436
Bromley, Robert G., see Fox, Anthony D., Hugh Boyd, and ———
Brown, Kevin M., and Ralph D. Morris, Investigator disturbance, chick movement, and aggressive behavior in Ring-billed Gulls, 140–152
Brown, Mike, see Ford, Cheri, and ———
Bubo spp., 103
virginianus, 111, 431, 432, 434, 615–628

Bubulcus ibis, 97
spp., 100
Bucco tamiata, 103
Bucher, Enrique H., see Navarro, Joaquín L., Mónica B. Bartella, and ———
Bunting, Indigo, see Passerina cyanea
Burtt, Edward H., Jr., and William E. Davis, Jr., Historic and taxonomic implications of recently found artwork in arithmetic books of students of Alexander Wilson, 193–213
Bustamante, Javier, see Hiraldo, Fernando, José A. Donázar, Olga Ceballos, Alejandro Travani, ———, and Martín Funes
Butchart, Duncan, see Mundy, Peter, ———, John Ledger, and Steven Piper
Buteo albonotatus, 720
jamaicensis, 271, 452–462, 525, 553, 615–628, 720
lagopus, 682
platypterus, 452–462
Butler, Robert W., and Gary W. Kaiser, Migration chronology, sex ratio, and body mass of Least Sandpipers in British Columbia, 413–422
Buzzard, Rough-legged, see Buteo lagopus
Buzzard-Eagle, Gery, see Geranoaetus melanoleucus
Cacholote, Brown, see Pseudoseisura lophotes
Calamospiza melanocorys, 709–718
Calcarius ornatus, 709–718
Calidris alpina, 131–139
mauri, 131, 413–422
minutilla, 131, 413–422
ruficollis, 132
spp., 102
Callipepla californica, 107, 679
gambelii, 262
spp., 101
Calypte anna, 566
Calyptorhynchus baudinii latirostris, 526
Campbell, R. Wayne, see Maples, Michael T., Denver W. Holt, and ———
Campylorhynchus brunneicapillus, 262, 763
Canachites canadensis, 107
Canis familiaris, 170, 592, 598, 600
latrans, 254, 255, 667–674
Canvasback, see Aythya valisineria
Capercaillie, Eurasian, see Tetrao urogallus
Caprimulgus carolinensis, 566
vociferus, 262, 720
Caracara, Crested, see Polyborus plancus
Cardellina rubrifrons, 721
Cardinal, Northern, see Cardinalis cardinalis
Cardinalis cardinalis, 45, 122–130, 367, 368, 701, 702
Carduelis flammea, 127, 128, 129
pinus, 122–130, 469, 720, 721
tristis, 122–130, 368, 701, 703
Carib, Green-throated, see Eulampis holosericeus
Purple-throated, see Eulampis jugularis
caribou, see Rangifer tarandus
Carmona, Roberto, Juan Guzmán, and Juan F. Elorduy, Hatching, growth, and mortality of Magnificent Frigatebird chicks in southern Baja California, 328–337
carp, see Cyprinus carpio
Carpococcyx spp., 102
Carpodacus mexicanus, 122–130, 165, 556
purpureus, 122–130
Casmerodius albus, 437–451
Castor canadensis, 262
Casuarius spp., 98
cat, domestic, see Felis silvestris
Catbird, Gray, see Dumetella carolinensis
catfish, channel, see Ictalurus punctatus
flathead, see Pylodictis olivaris
Catharacta maccormicki, 321, 323, 326
lonnbergi, 317–327
Cathartes aura, 42, 455, 720
spp., 100
Catharus guttatus, 701, 702, 720
ustulatus, 26–39
Catherpes mexicanus, 721
Catoptrophorus semipalmatus, 74
Catostomus clarki, 258, 261, 262
insignis, 258, 261, 262
Ceballos, Olga, see Hiraldo, Fernando, José A. Donázar, ———, Alejandro Travani, Javier Bustamante, and Martín Funes
censusing methods
bias in Christmas Bird Counts for feeder species, 122–130
Centrocercus urophasianus, 112, 113
Centropus spp., 102
Cepphus columba,

grylle, 398–403
Certhia americana, 127, 129, 195, 468, 702, 720
Cervus canadensis, 464
elaphus, 679
Chaetophractus villosus, 679
Chancellor, R. D., see Meyburg, B.-U., and ———
Chapman, Robert A., see Gibbons, David Wingfield, James B. Reid, and ———
Charadrius alexandrinus, 275–288
melodus, 287, 767–768, 768–769
vociferus, 131, 174–178, 709–718
wilsonia, 73–80
Chauna spp., 95, 100, 102
Chavez-Ramirez, Felipe, Sex-biased Kleptoparasitism of Hooded Mergansers by Ring-billed Gulls, 379–382
Chat, Yellow-breasted, see Icteria virens
chemoreception
in Sturnus vulgaris, 165–169
Chen caerulescens, 246, 382, 752–756
Chickadee, Black-capped, see Parus atricapillus
Carolina, see Parus carolinensis
Mountain, see Parus gambeli
chicken, see Gallus gallus
Chionis spp., 102
chipmunk, eastern, see Tamias striatus
Chlorostilbon auriceps, 19
canivetti, 19
Chordeiles minor, 42
Choriotis spp., 101
Chuck-will's-widow, see Caprimulgus carolinensis
Ciconia spp., 100
Cinclus mexicanus, 721, 722
Circus cyaneus, 452, 455
spp., 100
Cistothorus platensis, 709–718
Cladorhynchus leucocephalus, 132
Clamator spp., 102
Clangula hyemalis, 359
Clark, Larry, see Mason, J. Russell, and ———
Clench, Mary H., and John R. Mathias, The avian cecum: a review, 93–121
Clevelandia ios, 137
clutch size
in Myiopsitta monachus, 742–746
Cnemophilus loriae, 372
macgregorii, 372
Coccothraustes vespertinus, 127, 129
Cochlearius spp., 100
Cockatoos, White-tailed Black, see Calyptorhynchus baudinii latirostris
Coe, James, Eastern birds, reviewed, 388–389
Coereba flaveola, 592
Colaptes auratus, 44, 126, 128, 129, 262, 469, 471, 720
pitius, 679
Colinus cristatus,101
spp., 111
virginianus, 170, 312, 313, 761
Colius spp., 103
Collazo, Jaime A., see Zeller, Nanette S., and ———
Coluber constrictor, 262
spp., 619
Columba fasciata, 720
leucocephala, 479
livia, 112, 113, 115, 126, 128, 129, 165, 300
spp., 102
squamosa, 460, 727–733
Combs, Daniel L., and Leigh H. Fredrickson, Molt chronology of male Mallards wintering in Missouri, 359–365
community
comparison of forested and disturbed Florida pine scrub, 40–54
effect of Alopex lagopus on seabirds in Labrador, 397–412
Condor, California, see Gymnogyps californianus
Conepatus chinga, 678, 679
Confer, John L., and Richard T. Holmes, Neotropical migrants in undisturbed and human-altered forests of Jamaica, 577–589
Connor, Richard N., and D. Craig Rudolph, Losses of Red-cockaded Woodpecker cavity trees to southern pine beetles, 81–92
conservation
of breeding bird habitat in North Dakota, 709–718
Contopus borealis, 468, 471

pertinax, 721, 722
sordidulus, 468, 471, 721
Contreras-Balderas, Armando J., Juan A. García-Salas, and Jose I. Gonzáles-Rojas, Additional records of owls and wood warblers from Mexico, 765
Coot, American, see Fulica americana
Eurasian, see Fulica atra
Copsychus malabaricus, 311–328
Coracias benghalensis, 97
spp., 103
Coracina caeruleogrisea, 526
Coragyps atratus, 363, 751
Coriotis spp., 101
Cormorant, Brandt's, see Phalacrocorax penicillata
Double-crested, see Phalacrocorax auritus
Little, see Phalacrocorax niger
Corvus brachyrhynchos, 122–130, 170
corax, 125, 126, 128, 255, 285, 667–674, 720
spp., 103, 110
cottontail, see Sylvilagus audubonii
Coturnix coturnix, 97, 300, 592
spp., 101
Coulter, Malcolm C., review by, 190
cow, hereford, see Bos taurus
Cowbird, Brown-headed, see Molothrus ater
Shiny, see Molothrus bonariensis
coyote, see Canis latrans
crab, ghost, see Ocypode quadrata
Crane, Greater Sandhill, see Grus canadensis tabida
Sandhill, see Grus canadensis
Crax spp., 101
Creeper, Brown, see Certhia americana
Crex spp., 101
Cronin, Matthew A., see Pitocchelli, Jay, John Piatt, and ———
Crossbill, Red, see Loxia curvirostra
Crow, American, see Corvus brachyrhynchos
Cruz, Alexander, see Prather, John W., and ———
Crypturellus parvirostris, 98
spp., 98
Ctenomys sp., 679
Curlew, Eurasian, see Numenius arquata
Curry, Robert L., see Gómez, Juan E. Martínez, and ———
Cuthbert, Francesca, see Rissler, Leslie J., David N. Karowe, ———, and Brian Scholtens
Cyanocitta cristata, 44, 122–130, 170, 702
stelleri diademata, 720
Cyanocompsa parellina, 19
Cyanoliseus patagonus, 679
Cygnus spp., 100
Cyprinus carpio, 258, 261, 262
Dacelo spp., 103
Dahlsten, Donald L., see Kleintjes, Paula K., and ———
daily rhythym
of plasma corticosterone in Zonotrichia albicollis and Zonotrichia leucophrys, 296–305
Davidson, Nick, and Phil Rothwell (eds.), Disturbance to waterfowl on estuaries, reviewed, 774–775
Davis, William E., Jr., Dean of the birdwatchers, a biography of Ludlow Griscom, reviewed, 394–396
Davis, William E., Jr., reviews by, 773–774, 774–775, 775
Davis, William E., Jr., see Burtt, Edward H., Jr., and ———
deer, black-tailed, see Odocoileus hemionus
mule, see Odocoileus hemionus
Delichon urbica, 413
Dendragapus obscurus, 109
Dendrocygna spp., 217
Dendroica adelaidae, 482
caerulescens, 577–589, 765
coronata, 45, 51, 127, 129, 468, 701, 702, 704, 706, 720
discolor, 475–484, 577–589
graciae, 721
kirtlandii, 604
magnolia, 26–39, 580
nigrescens, 721
palmarum, 45, 51, 580, 587
petechia, 475–484, 765
pharetra, 482
pinus, 45, 48
pityophila, 482
plumbea, 482
tigrina, 580
vitellina, 482
detectability

of Columba squamosa after Hurricane Hugo, 727–733
Dickcissel, see Spiza americana
Dickinson, Vanessa M., Red imported fire ant predation on Crested Caracara nestlings in south Texas, 761–762
Didelphis virginianus, 170
diet
Buteo jamaicensis and Bubo virginianus as nocturnal-diurnal counterparts, 615–628
of breeding Anas cyanoptera in Arizona, 64–72
of breeding Haliaeetus leucocephalus, 258–274
of Geranoaetus melanoleucus in Patagonia, 675–685
of Myiopsitta monachus in Chicago, 510–517
of nesting Charadrius vociferous, 174–178
of Todus mexicanus, 181–182
Ovis aries carcass availability and use by Haliaeetus leucocephalus, 251–257
response by female Loxia curvirostra to carotenoid supplement, 555–557
winter food of Regulus satrapa, 558–561
Diomedea immutabilis, 384
spp., 100
Dipper, American, see Cinclus mexicanus
distribution
new species for Mexico, 765
of autumn migrants on the Isthmus of Tehuantepec, 26–39
of overwintering passerines in hardwood forests, 698–708
of raptors in Puerto Rico, 452–462
DNA sequencing
comparison of Pipilo and Spizella genera, 641–654
Dobkin, David S., Conservation and management of Neotropical migrant landbirds in the northern Rockies and Great Plains, reviewed, 773–774
Dodge, Anthony G., Adam J. Fry, Rachelle C. Blackwell, and Robert M. Zink, Comparison of phylogenies derived from two molecular data sets in the avian genera Pipilo and Spizella, 641–654
dog, domestic, see Canis familiaris
Dolichonyx oryzivorus, 709–718
Donázar, José A., see Hiraldo, Fernando, ———, Olga Ceballos, Alejandro Travani, Javier Bustamante, and Martín Funes
Dorosoma sp., 446
Dotterel, Red-kneed, see Erythrogonys cinctus
Dove, Collared, see Streptopelia decaocto
Mourning, see Zenaida macroura
Rock, see Columba livia
White-winged, see Zenaida asiatica
Zenaida, see Zenaida aurita
dowitcher, see Limnodromus spp.
Drobney, Ronald D., see Thompson, Jonathan E., and ———
Dromaius spp., 109, 110
Dryocopus pileatus, 127, 129
Duck, American Black, see Anas rubripes
Argentinian Ruddy, see Oxyura vittata
Black-headed, see Heteronettathalassornis atricapilla
Blue-billed, see Oxyura australis
Freckled, see Stictonetta naevosa
Maccoa, see Oxyura maccoa
Masked, see Oxyura dominica
Mexican, see Anas diazi, 548–551
Mottled, see Anas fulvigula maculosa
Musk, see Biziura lobata
Northern Ruddy, see Oxyura jamaicensis
Peruvian Ruddy, see Oxyura ferruginea
Ring-necked, see Aythya collaris
White-backed, see Thalassornis leuconotus
White-headed, see Oxyura leucocephala
Wood, see Aix sponsa
Dumetella carolinensis, 26–39, 368, 369, 378
Dunlin, see Calidris alpina
Dunn, Erica H., Bias in Christmas Bird Counts for species that visit feeders, 122–130
Dusicyon culpaeus, 681
Eagle, Bald, see Haliaeetus leucocephalus
Crested Serpent, see Spilornis cheela
Golden, see Aquila chrysaetos
ecology
Buteo jamaicensis and Bubo virginianus as dietary counterparts, 615–628

effect of Sphyrapicus varius on insect communities, 746–752
of Otus flammeolus in marginal habitat, 530–537
of stiff-tailed ducks (Anatidae: Oxyurini), 214–234
ectoparasitism
of Pseudoseisura lophotes and Anumbius annumbi by Philornis pici and Philornis seguyi, 734–738
Edge, W. Daniel, see Marr, N. Vern, ———, Robert G. Anthony, and Ray Valburg
editor's note
change in review editor, 396
egg
description for Mimodes graysoni, 551–555
predation on Charadrius melodus by Ocypode quadrata, 767–768
egg composition
intraspecific variation, 382–387
egg laying
effect of date on reproductive success in Myiopsitta monachus, 742–746
time of day in Sialia sialis, 377–379
Egret, Cattle, see Bubulcus ibis
Great, see Casmerodius albus
Snowy, see Egretta thula
Egretta spp., 100
thula, 437–451
tricolor, 7, 437–451
Elaphe obsoleta, 90
Eligmodontia typus, 679
elk, see Cervus canadensis
Elorduy, Juan F., see Carmona, Roberto, Juan Guzmán, and ———
Emison, W. B., C. M. Beardsell, and I. D. Temby, The biology and status of the Long-billed Corella in Australia, reviewed, 775
Empidonax minimus, 26–39
occidentalis, 720, 721
spp., 468
"traillii", 26–39
Emslie, Steven D., Nina Karnovsky, and Wayne Trivelpiece, Avian predation at penguin colonies on King George Island, Antarctica, 317–327
emu, see Dromaius spp.
Eolophus roseicapillus, 110
Epicrates inornatus, 525, 592, 600
Eremophila alpestris, 180, 709–718
Erythrogonys cinctus, 132
estimation procedure
total body electrical conductivity technique, 306–316
Eudocimus albus, 437–451
Eudromia elegans, 96, 98, 99, 114
spp., 98
Eudynamys scolopacea, 97
spp., 102
Eudyptes spp., 98
Eugenes fulgens, 721
Eulampis holosericeus, 566
jugularis, 566
Euphagus cyanocephalus, 126, 128, 129, 469, 471
Euphonia luteicapilla, 374
Euphonia, Yellow-crowned, see Euphonia luteicapilla
Eupodotis spp., 101
Eurynorhynchus spp., 101
Eurypyga helias, 101
spp., 95
Fair, Jeanne M., and Clinton K. Miller, The parasitic blow fly, Protocalliphora spatulata, in two new host species, 179–181
Fair, Jeanne M., Patricia L. Kennedy, and Lowell C. McEwen, Diet of nesting Killdeer in North Dakota, 174–178
Falco columbarius, 452–462, 566
mexicanus, 271
peregrinus, 452–462
sparverius, 452–462
spp., 95, 100
Falcon, Peregrine, see Falco peregrinus
Prairie, see Falco mexicanus
Fairly, Rob, ed., Blackburn's birds: the bird painting of Jemima Blackburn, reviewed, 568–569
Fedynich, Alan M., and Olin E. Rhodes, Jr., Mallard-like ducks in the Playa Lakes Region, 548–551
Felis silvestris, 170, 592, 598, 600
Fernandez, Renato, see Peterson, A. Townsend, Nina Ingle, and ———
Field, Rebecca, see Wilson, Karen A., ———, and Marcia H. Wilson
Finch, House, see Carpodacus mexicanus

Purple, see Carpodacus purpureus
Rosy, see Leucosticte arctoa
Zebra, see Taeniopygia guttata
Firewood-gatherer, see Anumbius annumbi
Flicker, Northern, see Colaptes auratus
Flores, Dan, see Bolen, Eric G., and ———
Flycatcher, Ash-throated, see Myiarchus cinerascens
Brown-crested, see Myiarchus tyrannulus
Cordilleran, see Empidonax occidentalis
Dusky-capped, see Myiarchus tuberculifer
Gray, see Tyrannus dominicensis
Great Crested, see Myiarchus crinitus
Least, see Empidonax minimus
Olive-sided, see Contopus borealis
Sulphur-bellied, see Myiodynastes luteiventris
"Trail's", see Empidonax "traillii"
Ford, Cheri, and Mike Brown, Unusual Marbled Murrelet nest, 178–179
Forpus passerinus, 742, 744
Fowl, Domestic, see Gallus domesticus
Fox, Anthony D., Hugh Boyd, and Robert G. Bromley, Diurnal activity budgets of pre-nesting Sandhill Cranes in arctic Canada, 752–756
fox, arctic, see Alopex lagopus
Culpeo, see Dusicyon culpaeus
gray, see Urocyon cinereoargenteus
red, see Vulpes vulpes
Franzreb, Kathleen E., see Hanula, James L., and ———
Fraser, James D., see Loegering, John P., ———, and Lisa L. Loegering
Fratercula arctica, 397–412 (Frontispiece)
spp., 102
Fredrickson, Leigh H., see Combs, Daniel L., and ———
Fregata magnificens, 328–337
spp., 100
Frigatebird, Magnificent, see Fregata magnificens
Fry, Adam J., see Dodge, Anthony G., ———, Rachelle C. Blackwell, and Robert M. Zink
Fry, C. Hilary, see Keith, Stuart, Emil K. Urban, and ———
Fulica americana, 261, 262
atra, 107, 386
spp., 101
Fulmar, Northern, see Fulmarus glacialis
Fulmarus glacialis, 398, 403
spp., 100
Funes, Martín, see Hiraldo, Fernando, José A. Donázar, Olga Ceballos, Alejandro Travani, Javier Bustamante, and ———
Gadwall, see Anas strepera
Galah, see Eophus roseicapillus
Galictis cuja, 678, 679
Gallus domesticus, 301
gallus, 643
spp., 93, 101
Gambusia holbrooki, 448
Gammonley, James H., Spring feeding ecology of Cinnamon Teal in Arizona, 64–72
García-Salas, Juan A., see Contreras-Balderas, Armando J., ———, and Jose I. Gonzáles-Rojas
Gates, J. Edward, see Karwowski, Kenneth, ———, and Lee H. Harper
Gavia spp., 98
Gehlbach, Frederick R., see McCallum, D. Archibald, ———, and Sophie W. Webb
genetics
divergence among Alaskan populations of Brachyramphus murrelets, 235–250
Geococcyx californianus, 262
spp., 102
Geothlypis trichas, 45, 368, 369, 577–589, 709–718
Geranoaetus melanoleucus, 675–685
Gibbons, David Wingfield, James B. Reid, and Robert A. Chapman, The new atlas of breeding birds in Britain and Ireland; 1988–1991, reviewed, 191
Glareola spp., 102
Glaucidium brasilianum, 5, 7, 9, 12, 19, 21
gnoma, 7, 20, 721 (Frontispiece)
griseiceps, 2, 3, 4 (Frontispiece), 7–25
hardyi, 1–6 (Frontispiece), 7–25
jardinii, 1, 5, 7, 8
minutissimum, 1–6 (Frontispiece), 7–25
palmarum, 1–6 (Frontispiece), 7–25
parkeri sp. nov., 1–6 (Frontispiece), 7–25
passerinum, 9
peruanum, 5

sanchezi, 2, 3, 4 (Frontispiece), 7–25
spp., 103
Gnatcatcher, Blue-gray, see Polioptila caerulea
White-lored, see Polioptila albiloris
Godwit, Marbled, see Limosa fedoa
Goldcrest, see Regulus regulus
Golden-Plover, Greater, see Pluvialis apricaria
Goldfinch, American, see Carduelis tristis
Gómez, Juan E. Martínez, and Robert L. Curry, First description of the nest and eggs of the Socorro Mockingbird, 551–555
Gonzáles-Rojas, Jose I., see Contreras-Balderas, Armando J., Juan A. García-Salas, and ———
Goose, Canada, see Branta canadensis
Egyptian, see Alopochen aegyptiacus
Snow, see Chen caerulescens
Spurwinged, see Plectropterus gambensis
White-fronted, see Anser albifrons
Goshawk, Northern, see Accipiter gentilis
Gowaty, Patricia Adair, see Plissner, Jonathan H., and ———
Grackle, Common, see Quiscalus quiscula
Great-tailed, see Quiscalus mexicanus
Graedel, Susannah K., and Robert E. Loveland, Seasonal and diurnal mass variation in Black-capped Chickadees and White-throated Sparrows, 723–727
Graves, Gary R., Sequence of plumage evolution in the Standardwing Bird of Paradise, 371–373
Grebe, Little, see Tachybaptus ruficollis
Greenberg, Cathryn H., Lawrence D. Harris, and Daniel G. Neary, A comparison of bird communities in burned and salvage-logged, clearcut, and forested Florida sand pine scrub, 40–54
Greenshank, see Tringa nebularia
grison, see Galictis cuja
Grosbeak, Black-headed, see Pheucticus melanocephalus
Evening, see Coccothraustes vespertinus
Pine, see Pinicola enucleator
Groth, Jeffrey G., Evolutionary differentiation in morphology, vocalization, and allozymes among nomadic sibling species in the North American Red Crossbill (Loxia curvirostra) complex, reviewed, 389–391
Grouse, Alberta Spruce, see Canachites canadensis
Blue, see Dendragapus obscurus
Red, see Lagopus lagopus scoticus
Ruffed, see Bonasa umbellus
Sage, see Centrocercus urophasianus
Willow, see Lagopus lagopus lagopus
growth
of Fregata magnificens chicks, 328–337
Grubb, Teryl, Food habits of Bald Eagles breeding in the Arizona desert, 258–274
Grus canadensis, 752–756
canadensis tabida, 667–674, 766
spp., 101
Guillemot, Black, see Cepphus grylle
Gull, California, see Larus californicus
Glaucous-winged, see Larus glaucescens
Great Black-backed, see Larus marinus
Herring, see Larus argentatus
Kelp, see Larus dominicanus
Ring-billed, see Larus delawarensis
Slaty-backed, see Larus schistisagus
Western, see Larus occidentalis
Guzmán, Juan, see Carmona, Roberto, ———, and Juan F. Elorduy
Gygis spp., 102
Gymnogyps californianus, 256
Gymnorhina spp., 103
Gyps spp., 100
Gypohierax spp., 100
habitat
breeding
loss of Picoides borealis cavity trees to Dendroctomus frontalis, 81–92
conservation
for breeding birds in North Dakota, 709–718
human-altered
use by Neotropical migrants in Jamaica, 577–589
selection
in Nearctic-Neotropic autumn migrants, 26–39
species richness
in relation to isolation in stands of aspen, 463–474

use
by wintering Scolopax minor, 686–697
in relation to edge in an irrigated forest, 365–371
of disturbed Florida pine scrub by breeding and wintering birds, 40–45
of wetlands by breeding and postbreeding Anas platyrhynchos, 55–63
Haematopus fuliginosus, 629–640
longirostris, 629–640
moquini, 637
ostralegus, 637
Haliaeetus leucocephalus, 251–257, 258–274
spp., 100
Hall, George A., reviews by, 191, 394–396
Halliday, Tim, ed., Animal behavior, reviewed, 393–394
Handford, Paul T., see Lozano, George A., and ———
Hannon, Susan J., see Martin, Kathy, Andrew G. Horn, and ———
Hanula, James L., and Kathleen E. Franzreb, Arthropod prey of nestling Red-cockaded Woodpeckers in the upper coastal plain of South Carolina, 485–495
hare, European, see Lepus europaeus
Harper, Lee H., see Karwowski, Kenneth, J. Edward Gates, and ———
Harrier, Northern, see Circus cyaneus
Harris, Lawrence, D., see Greenberg, Cathryn H., ———, and Daniel G. Neary
Hartshorn, Gary S., see McDade, Lucinda A., Jamaljit S. Bawa, Henry A. Hespendheide, and ———
hatching
of Fregata magnificens chicks, 328–337
Hawk, Broad-winged, see Buteo platypterus
Cooper's, see Accipiter cooperii
Red-tailed, see Buteo jamaicensis
Sharp-shinned, see Accipiter striatus
Zone-tailed, see Buteo albonotatus
Hein, Dale, see Turchi, Gail M., Patricia L. Kennedy, Dean Urban, and ———
Heinrich, Bernd, and Ross Bell, Winter food of a small insectivorous bird, the Golden-crowned Kinglet, 558–561
Heliornis spp., 101
Helmitheros spp., 700
vermivorus, 48, 54, 26–39, 580
Heron, Great Blue, see Ardea herodias
Tricolored, see Egretta tricolor
Herpestes auropunctatus, 592, 600
Hespendheide, Henry A., see McDade, Lucinda A., Jamaljit S. Bawa, ———, and Gary S. Hartshorn
Heteronetta atricapilla, 214–234
Hill, Geoffrey E., and Craig W. Benkman, Exceptional response by female Red Crossbills to dietary carotenoid supplementation, 555–557
Hill, Wendy L., Intraspecific variation in egg composition, 382–387
Himantopus himantopus, 132
Hiraldo, Gernando, José A. Donázar, Olga Ceballos, Alejandro Travani, Javier Bustamante, and Martín Funes, Breeding biology of a Grey Eagle-Buzzard population in Patagonia, 675–685
Hirundo pyrrhonota, 761
history
of artwork of students of Alexander Wilson, 193–213
Hoatzin, see Opisthocomus hoatzin
Holm, Daniel J., see Bellrose, Frank C., and ———
Holmes, Richard T., see Confer, John L., and ———
Holt, Denver W., see Maples, Michael T., ———, and R. Wayne Campbell
Honeyguide, Lesser, see Indicator minor
Horn, Andrew G., see Martin, Kathy, ———, and Susan J. Hannon
Howell, Steve N. G., and Mark B. Robbins, Species limits of the Least Pygmy-Owl (Glaucidium minutissimum) complex, 7–25
Howell, Steve N. G., see Robbins, Mark B., and ———
Hummingbird, Anna's see Calypte anna
Black-chinned, see Archilochus alexandri
Broad-tailed, see Selasphorus platycercus
Magnificent, see Eugenes fulgens
Ruby-throated, see Archilochus colubris
Hylocichla mustelina, 26–39, 369, 738–741
Hyman, Jeremy, and Stephen Pruett-Jones,

Natural history of the Monk Parakeet in Hyde Park, Chicago, 510–517
Ibis, White, see Eudocimus albus
Ictalurus punctatus, 258, 261, 262
Icteria virens, 26–39
Icterus galbula, 374, 566
parisorum, 721
Ictinia mississippiensis, 762
Igl, Lawrence D., see Johnson, Douglas H., and ———
Indicator minor, 103
information for authors, 574–575
Ingle, Nina, see Peterson, A. Townsend, ———, and Renato Fernandez
Ivey, Gary L., see Littlefield, Carroll D., and ———
Ivey, Gary L., see Scheuering, Eric J., and ———
Jacana spp., 102
jackrabbit, see Lepus spp.
black-tailed, see Lepus californicus
Jackson, Jerome A., review by, 569–571
Jay, Blue, see Cyanocitta cristata
Florida Scrub, see Aphelocoma caerulescens coerulescens
Gray, see Perisoreus canadensis
Gray-breasted, see Aphelocoma ultramarina
Scrub, see Aphelocoma coerulescens
Stellar's, see Cyanocitta stelleri diademata
Jehl, Joseph R., Jr., and Ned K. Johnson (eds.), A century of avifaunal change in western North America, reviewed, 189–190
Jenni, Lukas, and Raffael Winkler, Moult and aging of European passerines, reviewed, 771–772
Johnson, Douglas H., and Lawrence D. Igl, Contribution of the conservation reserve program to populations of breeding birds in North Dakota, 709–718
Johnson, Ned K., see Jehl, Joseph R., Jr., and ———
Junco, Dark-eyed, see Junco hyemalis
Yellow-eyed, see Junco phaeonotus
Junco hyemalis, 122–130, 193–213, 367, 369, 468, 641–654
phaeonotus, 720
Justice, Michael J., and Cheryl A. Logan, The effects of exogenous testosterone on male Northern Mockingbirds during the breeding season, 538–542
Kaiser, Gary W., see Butler, Robert., and ———
Kakapo, see Strigops habroptilus
Karnovsky, Nine, see Emslie, Steven D., ———, and Wayne Trivelpiece
Karowe, David N., see Rissler, Leslie J., ———, Francesca Cuthbert, and Brian Scholtens
Karwowski, Kenneth, J. Edward Gates, and Lee H. Harper, Common Terns nesting on navigational aids and natural islands in the St. Lawrence River, New York, 423–436
Keith, Stuart, Emil K. Urban, and C. Hilary Frey, The birds of Africa, Volume IV, reviewed, 186–187
Kennedy, Patricia L., see Fair, Jeanne M., ———, and Lowell C. McEwen
Kennedy, Patricia L., see Turchi, Gail M., ———, Dean Urban, and Dale Hein
Kestrel, American, see Falco sparverius
Killdeer, see Charadrius vociferus
Kinglet, Golden-crowned, see Regulus satrapa
Ruby-crowned, see Regulus calendula
Kinosternon sonoriense, 261, 262
Kite, Mississippi, see Ictinia mississippiensis
Kittiwake, Black-legged, see Rissa tridactyla
Kleintjes, Paula K., and Donald L. Dahlsten, Within-season trends in the foraging behavior of the Mountain Chickadee, 655–666
Kochert, Michael N., see Marti, Carl D., and ———
Koel, Common, see Eudynamys scolopacea
Krementz, David G., John T. Seginak, and Grey W. Pendleton, Habitat use at night by wintering American Woodcock in coastal Georgia and Virginia, 686–697
Kricher, John C., review by, 571–572
Lagopus lagopus, 107, 108, 109, 113, 496–509
lagopus lagopus, 106, 496
lagopus scoticus, 106, 113, 496
leucurus, 506
mutus, 107, 111

Lampe, Kevin T, see Marra, Peter P., ———, and Bruce L. Tedford
landscape characteristics
of Picoides borealis cluster sites, 603–614
Lanius excubitor, 764
ludovicianus, 762–764
minor, 764
senator, 764
Lapwing, see Vanellus vanellus
Redwattled, see Vanellus indicus
Lark, Horned, see Eremophila alpestris
Larus argentatus, 140, 141, 150, 432
californicus, 285
delawarensis, 140–152, 379–382, 431, 435
dominicanus, 317–327
glaucescens, 140
marinus, 141, 398, 406, 407
occidentalis, 321, 325, 326
schistisagus, 141
spp., 102
Latta, Steven C., Joseph M. Wunderle, Jr., Esteban Terranova, and Michelle Pagán, An experimental study of nest predation in a subtropical wet forest following hurricane disturbance, 590–602
Laughlin, Sally, review by, 391
Lauro, Brook, and Erica Nol, Feeding behavior, prey selection, and bill size of Pied and Sooty oystercatchers in Australia, 629–640
Ledger, John, see Mundy, Peter, Duncan Butchart, ———, and Steven Piper
Lepomis spp., 262
Leptoptilos spp., 100
Lepus californicus, 262
europaeus, 675–685
spp., 261, 619
Leucosticte arctoa, 180
Limnodromus spp., 131
Limosa fedora, 131
Linder, Eric T., and Eric K. Bollinger, Depredation of artificial Ovenbird nests in a forest patch, 169–174
Littlefield, Carroll D., Demographics of a declining flock of Greater Sandhill Cranes in Oregon, 667–674
Littlefield, Carroll D., and Gary Ivey, An unusual record of Sandhill Crane philopatry, 766
Livezey, Bradley C., Phylogeny and comparative ecology of stiff-tailed ducks (Anatidae: Oxyurini), 214–234
lizard, see Anolis spp.
Loegering, John P., James D. Fraser, and Lisa L. Loegering, Ghost crab preys on a Piping Plover chick, 768–769
Loergering, Lisa L., see Loegering, John P., James D. Fraser, and ———
Logan, Cheryl A., see Justice, Michael J., and ———
Longspur, Chestnut-collared, see Calcarius ornatus
Lophodytes cucullatus, 758, 379–382
Lophorina superba, 528, 372
Losito, Michael P., and Guy A. Baldassarre, Wetland use by breeding and postbreeding female Mallards in the St. Lawrence River Valley, 55–63
Loveland, Robert E., see Graedel, Susannah K., and ———
Loxia curvirostra, 389–391, 469, 555–557, 720, 721
Lozano, George A., and Paul T. Handford, A test of an assumption of delayed plumage maturation hypotheses using female Tree Swallows, 153–164
Lyrebird, Superb, see Menura novaehollandiae
Macronectes giganteus, 317–327
halli, 323
Magpie, Black-billed, see Pica pica
Mallard, see Anas platyrhynchos
Maples, Michael T., Denver W. Holt, and R. Wayne Campbell, Ground nesting Long-eared Owls, 563–565
Margarops fuscatus, 525, 592, 598, 600
Marr, N. Vern, W. Daniel Edge, Robert G. Anthony, and Ray Valburg, Sheep carcass availability and use by Bald Eagles, 251–257
Marra, Peter P., Kevin T. Lampe, and Bruce L. Tedford, Plasma corticosterone levels in two species of Zonotrichia sparrows under captive and free-living conditions, 296–305
Marshall, Joe T., Birds of coniferous forest on Mount Graham, Arizona, 719–723

Marti, Carl D., and Michael N. Kochert, Are Red-tailed Hawks and Great Horned Owls diurnal-nocturnal dietary counterparts? 615–628
Martin, Kathy, Andrew G. Horn, and Susan J. Hannon, The calls and associated behavior of breeding Willow Ptarmigan in Canada, 496–509
Mason, J. Russell, and Larry Clark, Capsaicin detection in trained European Starlings: the importance of olfactory and trigeminal chemoreception, 165–169
Mathias, John R., see Clench, Mary H., and ———
McCallum, D. Archibald, Frederick R. Gehlbach, and Sophie W. Webb, Life history and ecology of Flammulated Owls in a marginal New Mexico population, 530–537
McDade, Lucinda A., Jamaljit S. Bawa, Henry A. Hespendheide, and Gary S. Hartshorn (eds.), La Selva, ecology and natural history of a Neotropical rain forest, reviewed, 772–773
McDougall-Schackleton, Elizabeth A., and Raleigh J. Robertson, Mate guarding tactics used by Great Crested Flycatchers, 757–761
McEwen, Lowell C., see Fair, Jeanne M., Patricia L. Kennedy, and ———
McNeil, Raymond, see Thibault, Michel, and ———
McPeek, Gail A., ed., The birds of Michigan, reviewed, 573
Meadowlark, Eastern, see Sturnella magna
Western, see Sturnella neglecta
Meek, Susan B., and Raleigh J. Robertson, Time of day of egg laying by Eastern Bluebirds, 377–379
meetings
Southern Hemisphere Ornithological Congress, 54
Wilson Ornithological Society, 38
Megalaima spp., 103
Melanerpes carolinus, 44, 126, 128, 129
formicivorus, 721
spp., 103
uropygialis, 262
Melanitta nigra, 103
spp., 100
Meleagris gallopavo, 262, 300, 720
Melospiza lincolnii, 193–213
melodia, 122–130, 368, 541, 651
Menura novaehollandiae, 103
Mephitis mephitis, 170, 262, 276, 284
Merganser, Common, see Mergus merganser
Hooded, see Lophodytes cucullatus
Mergus merganser, 262, 354, 381
spp., 95, 100
Merlin, see Falco columbarius
Merola, Michele, Fruit in the diet of nestlings of the Puerto Rican Tody, a tropical insectivore, 181–182
Merops spp., 103
Metallura odomae, 169
Meyburg, B.-U., and R. D. Chancellor, Raptor conservation today, reviewed, 773
Micrathene whitneyi, 721
Micropterus dolomieui, 262
spp., 262
Microtus spp., 619
Miller, Clinton K., see Fair, Jeanne M., and ———
Milvago chimango, 679
Milvus spp., 100
Mimodes graysoni, 551–555
Mimus polyglottos, 125, 127, 129, 262, 538–542, 551
Mniotilta varia, 577–589
Mockingbird, Northern, see Mimus polyglottos
Socorro, see Mimodes graysoni
mollie, sailfin, see Poecilia latipinna
Molothrus ater, 127, 129, 172, 378, 475, 709–718
bonariensis, 475
molt
in male Anas platyrhynchos, 359–365
in male Aythya valisineria, 338–358
mongoose, Indian, see Herpestes auropunctatus
Morone mississippiensis, 262, 266
morphology
bill size of Haematopus longirostris and Haematopus fuliginosus, 629–640
of Alaskan populations of Brachyramphus murrelets, 235–250

Morris, Ralph D., see Brown, Kevin M., and ———
mortality
of Fregata magnificens chicks, 328–337
Morton, Eugene S., see Warkentin, Ian G., and ———
mosquitofish, see Gambusia holbrooki
Motacilla cinerea, 97
spp., 103
mouse, see Peromyscus spp.
deer, see Peromyscus maniculatus
movement
of Calidris alpina on wintering grounds, 131–139
Mundy, Peter, Duncan Butchart, John Ledger, and Steven Piper, The vultures of Africa, reviewed, 392–393
Murre, Common, see Uria aalge
Thick-billed, see Uria lomvia
Murrelet, Kittlitz's, see Brachyramphus marmoratus
Marbled, see Brachyramphus marmoratus
muskrat, see Ondatra zibethicus
Mycteria americana, 446
spp., 100
Myiarchus cineracens, 721
crinitus, 26–39, 44, 48, 51, 757–761
tuberculifer, 721
tyrannulus, 566
Myioborus pictus, 721
Myiodynastes luteiventris, 721 (Frontispiece)
Myiopsitta monachus, 510–517, 742–746
Myocastor coypus, 254
natural history
of Myiopsitta monachus in Hyde Park, Chicago, 510–517
of Otus flammeolus in marginal habitat, 530–537
Navarro, Joaquín L., Mónica B. Bartella, and Enrique H. Bucher, Effects of laying date, clutch size, and communal nest size on the reproductive success of Monk Parakeets, 742–746
Neary, Daniel. G., see Greenberg, Cathryn H., Lawrence D. Harris, and ———
Nelson, Coleen H., The downy waterfowl of North America, reviewed, 187–188
Neophron spp., 100
Neotoma spp., 261, 262, 619
Neotropical migrants
habitat selection on the Isthmus of Tehuantepec, 26–39
use of undisturbed and human-altered forests in Jamaica, 577–589
Nerodia compressicauda, 479
nest
of Mimodes graysoni, 551–555
predation following hurricane disturbance, 590–602
predation of Grus canadensis tabida in Oregon, 667–674
nest site
two-box preference in Sialia sialis, 289–295
use of navigational aids and islands by Sterna hirundo, 423–436
nesting
behavior of Amazona vittata, 518–529
Picoides borealis cavity tree destruction by Dendroctonus frontalis, 81–92
record for Quiscalus mexicanus in Oregon, 562–563
success of Grus canadensis tabida in Oregon, 667–674
unusual structure for Brachyramphus marmoratus, 178–179
nestling
arthropod prey of Picoides borealis, 485–495
movement of Larus delawarensis chicks in response to human disturbance, 140–152
Nestor spp., 102
Nettapus coromandelianus, 97
spp., 100
Nettleship, D. N., see Birkhead, T. R., and ———
Night-Heron, Black-crowned, see Nycticorax nycticorax
Nighthawk, Common, see Chordeiles minor
Nol, Erica, see Lauro, Brook, and ———
Nomonyx dominicus, 214–234
Nores, Ana I., Botfly ectoparasitism of the Brown Cacholote and the Firewood-gatherer, 734–738
Nothoprocta cinerascens, 98
Nothura maculosa, 99
spp., 98
Notornis mantelli, 110

Numenius arquata, 131, 137
phaeopus, 74
spp., 102
Numida spp., 101
Nuthatch, Brown-headed, see Sitta pusilla
Pygmy, see Sitta pygmaea
Red-breasted, see Sitta canadensis
White-breasted, see Sitta carolinensis
nutria, see Myocastor coypus
Nycticorax nycticorax, 432, 434
spp., 100
Nyctidromus spp., 103
Oceanodroma furcata, 384
leucorhoa, 100, 384, 398
Ocypode quadrata, 767–768, 768–769
Odocoileus hemionus, 254, 256, 464
Oldsquaw, see Clangula hyemalis
olfaction
role in chemoreception in Sturnus vulgaris, 165–169
Ondatra zibethica, 262
Opisthocomus hoatzin, 102, 109, 110
spp., 95, 97, 102
Oporornis formosus, 26–39
tolmiei, 464
opossum, Virginia, see Didelphis virginianus
Oriole, Northern, see Icterus galbula
Scott's, see Icterus parisorum
Oryctolagus cuniculus, 675–685
Osprey, see Pandion haliaetus
Otis spp., 101
Otus asio, 530–537
cooperi, 21
flammeolus, 530–537, 720
kennicottii, 21, 531, 721
nudipes, 452–462
seductus, 21
Ovenbird, see Seiurus aurocapillus
Ovis aries, 251–257, 679
Owl, Burrowing, see Speotyto cunicularia
Elf, see Micrathene whitneyi
European Little, see Athene noctua
Flammulated, see Otus flammeolus
Great Horned, see Bubo virginianus
Northern Spotted, see Strix occidentalis caurina
Short-eared, see Asio flammeus
Spotted, see Strix occidentalis
Tawny, see Strix aluco
Owlet, Spotted, see Athene brama
Oxyura australis, 214–234
dominica, 215
ferruginea, 214–234
jamaicensis, 214–234
leucocephala, 214–234
maccoa, 214–234
vittata, 214–234
Oystercatcher, African Black, see Haematopus moquini
European, see Haematopus ostralegus
Pied, see Haematopus longirostris
Sooty, see Haematopus fuliginosus
Pagán, Michelle, see Latta, Steven C., Joseph M. Wunderle, Jr., Esteban Terranova, and ———
Page, Gary W., see Warnock, Nils, ———, and Lynne E. Stenzel
Pagophila spp., 102
Palila, see Loxioides bailleui
Pandion haliaetus, 452–462
spp., 100
Parakeet, Monk, see Myiopsitta monachus
parasite
two new host species for Protocalliphora spatulata, 179–181
Parker, Patricia G., review by, 392–393
Parkes, Kenneth C., reviews by, 388–389, 568–569, 771–772
Parotia sp., 372
Parrot, Bahama, see Amazona leucocephala bahamensis
Puerto Rican, see Amazona vittata
Red-rumped, see Psephotus haematonotus
parrot, see Amazona spp.
Parrotlet, Green-rumped, see Forpus passerinus
Partridge, Gray, see Perdix perdix
Parula americana, 580
pitiayumi, 553
Parula, Northern, see Parula americana
Tropical, see Parula pitiayumi
Parus atricapillus, 122–130, 367, 369, 468, 470, 723–727
bicolor, 126, 128, 129, 367, 369, 542–547, 701, 702, 704
carolinensis, 122–130, 542–547, 701, 701, 704
gambeli, 467, 468, 469, 531, 655–666, 720 (Frontispiece)

spp., 103
wollweberi, 721
Passer agrestis, 206, 207
domesticus, 93, 122–130, 306–316
spp., 103
Passerculus sandwichensis, 179–181, 709–718
Passerella iliaca, 650, 702
Passerina cyanea, 26–39, 193–213, 368, 582
Paton, Peter W. C., Breeding biology of Snowy Plovers at Great Salt Lake, Utah, 275–288
Pavo spp., 101
peccary, collared, see Tayassu tajacu
Pelecanus spp., 100
Pendleton, Grey W., see Krementz, David G., John T. Seginak, and ———
Penguin, Adelie, see Pygoscelis adeliae
Gentoo, see Pygoscelis papua
Jackass, see Spheniscus demersus
King, see Aptenodytes patagonicus
Perdix perdix, 165
Perisoreus canadensis, 468
Peromyscus maniculatus, 409
spp., 262, 619
Perry, Sue A., review by, 772–773
Petersen, Wayne R., see Veit, Richard R., and ———
Peterson, A. Townsend, Nina Ingle, and Renato Fernandez, Notes on the nesting behavior of the White-bellied Woodpecker, 182–184
Petrel, Giant, see Macronectes giganteus and Macronectes halli
Peucedramus taeniatus, 721, 722
Pewee, Greater, see Contopus pertinax
Phaethon spp., 100
Phalacrocorax niger, 97
penicillatus, 321, 326
spp., 100
Phalaenoptilus nuttallii, 721 (Frontispiece)
spp., 103
Phalarope, Red-necked, see Phalaropus lobatus
Phalaropus lobatus, 112
Phasianus colchicus, 122, 128, 129
spp., 111, 619
Pheasant, Ring-necked, see Phasianus colchicus
Pheucticus melanocephalus, 720
Philornis pici, 734–738
seguyi, 734–738
Phodilus spp., 102
Phoebe, Eastern, see Sayornis phoebe
Phoenicopterus spp., 100
Phoeniculus purpureus, 375
Phyllotis darwini, 679
phylogeny
comparison of Pipilo and Spizella based on molecular data, 641–654
Phyrgilus gayi, 679
physiology
plasma corticosterone levels in Zonotrichia albicollis and Zonotrichia leucophrys, 296–305
Piatt, John, see Pitocchelli, Jay, ———, and Matthew A. Cronin
Pica pica, 127, 129, 386
Picoides borealis, 81–92, 485–495, 603–614
pubescens, 44, 122–130, 367, 369, 468
stricklandi, 721 (Frontispiece)
villosus, 122–130, 468, 471, 720
Picus viridis, 103
Pigeon, Band-tailed, see Columba fasciata
Scaly-naped, see Columba squamosa
White-crowned, see Columba leucocephala
Pinicola enucleator, 127, 128, 129
Pintail, Northern, see Anas acuta
Piper, Steven, see Mundy, Peter, Duncan Butchart, John Ledger, and ———
Pipilo aberti, 641–654
albicollis, 641–654
chlorurus, 641–654
crissalis, 641–654
erythrophthalmus, 45, 47, 48, 127, 129, 193–213, 368, 553, 701, 702, 721
fuscus, 641–654
ocai, 651
Pipit, American, see Anthus rebescens
Piranga flava, 720
ludoviciana, 720
olivacea, 368, 369
rubra, 45, 48
Pitocchelli, Jay, John Piatt, and Matthew A. Cronin, Morphological and genetic divergence among Alaskan populations of Brachyramphus murrelets, 235–250
Pituophis melanoleucus, 536

Platalea spp., 100
Plectropterus gambensis, 108
Plissner, Jonathan H., and Patricia Adair Gowaty, Eastern Bluebirds are attracted to two-box sites, 289–295
Plover, Black-bellied, see Pluvialis squatarola
Piping, see Charadrius melodus
Snowy, see Charadrius alexandrinus
Wilson's, see Charadrius wilsonia
plumage
delayed maturation in female Tachycineta bicolor, 153–164
evolution in Semioptera wallacii, 371–373
Pluvialis apricaria, 131
spp., 102
squatarola, 131, 137
Podiceps spp., 98
Poecilia latipinna, 448
Poephila spp., 103
Polemaetus spp., 100
Polioptila albilorus, 374
caerulea, 44, 48, 721
Polyborus plancus, 682, 761–762
spp., 100
Pooecetes gramineus, 709–718
Poorwill, Common, see Phalaenoptilus nuttallii
Porphyrio spp., 101
Power, Dennis M., (ed.), Current ornithology, Volume 11, reviewed, 192
Prairie-Chicken, Attwater's, see Tympanuchus cupido attwateri
Prather, John W., and Alexander Cruz, Breeding biology of Florida Prairie Warblers and Cuban Yellow Warblers, 475–484
predation
at penguin colonies on King George Island, Antarctica, 317–327
effect of Alopex lagopus on seabird communities in Labrador, 397–412
effect of simulation on mixed species flocks, 542–547
of artificial Seiurus aurocapillus nests, 169–174
of Tyrannus dominicensis on Eulampis hummingbird, 565–567
on Charadrius melodus chick by Ocypode quadrata, 768–769
on Charadrius melodus eggs by Ocypode quadrata, 767–768
on Polyborus plancus by Solenopsis invicta, 761–762
predator-prey
relationship between Charadrius wilsonia and Uca cumulanta, 73–80
prey
of nestling Picoides borealis, 485–495
selection by Haematopus longirostris and Haematopus fuliginosus, 629–649
proceedings
seventy-sixth annual meeting, 776–789
Procyon lotor, 170, 276, 284, 479, 667–674
Protocalliphora spatulata, 179–181
Protonotaria citrea, 374–376, 580, 765
Pruett-Jones, Stephen, see Hydman, Jeremy, and ———
Psaltriparus minimus, 721
Pseudoseisura lophotes, 734–738
Psophia spp., 101
Ptarmigan, Norwegian Rock, see Lagopus mutus
Willow, see Lagopus lagopus
White-tailed, see Lagopus leucurus
Pterodroma spp., 100
Pterocles spp., 102
Ptiloris sp., 372
Puffin, Atlantic, see Fratercula arctica
Puffinbird, Spotted, see Bucco tamiata
Puffinus auricularis, 553
griseus, 384
spp., 100
tenuirostris, 384
Pygmy-Owl, Amazonian, see Glaucidium hardyi
Andean, see Glaucidium jardinii
Brazilian, see Glaucidium minutissimum
Central American, see Glaucidium griseiceps
Colima, see Glaucidium palmarum
Eurasian, see Glaucidium passerinum
Ferruginous, see Glaucidium brasilianum
Least, see Glaucidium minutissimum
Northern [Pygmy Owl], see Glaucidium gnoma
Subtropical, see Glaucidium parkeri
Tamaulipas, see Glaucidium sanchezi
Pygoscelis adeliae, 317–327
papua, 98, 317–327

Pylodictis olivaris, 254, 261, 262
Pyrrhura picta amazonum, 7
Quail, California, see Callipepla [Lophortyx] californica
  Common, see Coturnix coturnix
  Gambel's, see Callipepla gambelii
  Japanese, see Coturnix coturnix
Quiscalus mexicanus, 262, 375, 562–563
  quiscula, 125, 127, 368, 566
rabbit, brush, see Sylvilagus bacmani
  European, see Oryctolagus cuniculus
racer, see Coluber constrictor
racoon, see Procyon lotor
Rangifer tarandus, 755
rat, see Rattus sp.
  black, see Rattus rattus
Rattus rattus, 592, 597
  sp., 479
  spp., 525
Raven, Common, see Corvus corax
Razorbill, see Alca torda
record
  new species for Mexico, 765
Recurvirostra novaehollandiae, 132
Redhead, see Aythya americana
Redpoll, Common, see Carduelis flammea
Redshank, see Tringa totanus
Redstart, American, see Setophaga ruticilla
  Painted, see Myioborus pictus
Regulus calendula, 44, 51, 127, 129, 468, 469, 701, 720, 721
  regulus, 558
  satrapa, 558–561, 701, 702, 704, 720
Reid, James B., see Gibbons, David Wingfield, ———, and Robert A. Chapman
Reithrodon auritus, 679
Rhea spp., 98
Rhodes, Olin E., Jr., see Fedynich, Alan M., and ———
Rhynchotus spp., 98
Rhynochetos spp., 101
ringtail, see Bassariscus astutus
Rising, J. D., review by, 389–391
Rissa tridactyla, 238, 247, 398, 406
Rissler, Leslie J., David N. Karowe, Francesca Cuthbert, and Brian Scholtens, The influence of Yellow-bellied Sapsuckers on local insect community structure, 746–752
Rivera-Milán, Frank F., Detectability and population density of Scaly-naped Pigeons before and after Hurricane Hugo in Puerto Rico and Vieques Island, 727–733
Rivera-Milán, Frank F., Distribution and abundance of raptors in Puerto Rico, 452–462
Roadrunner, Greater, see Geococcyx californianus
Robertson, Raleigh J., see MacDougall-Schackleton, Elizabeth A., and ———
Robertson, Raleigh J., see Meek, Susan B., and ———
Robbins, Mark B., and Steve N. G. Howell, A new species of Pygmy-Owl (Strigidae: Glaucidium) from the eastern Andes, 1–6
Robbins, Mark B., see Howell, Steve N. G., and ———
Robin, American, see Turdus migratorius
  Clay-colored, see Turdus grayii
Roby, Daniel D., see Asch, Andreas, and ———
Roller, Indian, see Coracias benghalensis
Ross, Bradley D., see Yahner, Richard H., and ———
Rothwell, Phil, see Davidson, Nick, and ———
Rudolph, D. Craig, see Conner, Richard N., and ———
Sagittarius serpentarius, 95, 100
  spp., 101
Sandpiper, Least, see Calidris minutilla
  Spotted, see Actitis macularia
  Upland, see Bartramia longicauda
  Western, see Calidris mauri
Sapsucker, Red-naped, see Sphyrapicus nuchalis
  Yellow-bellied, see Sphyrapicus varius
Sayornis phoebe, 51, 701, 702
Scaup, Greater, see Aythya marila
  Lesser, see Aythya affinis
Scheuering, Eric J., and Gary L. Ivey, First nesting record of the Great-tailed Grackle in Oregon, 562–563
Scholtens, Brian, see Rissler, Leslie J., David N. Karowe, Francesca Cuthbert, and ———

Schriml, Lynn M., see Picman, Jaroslav, and ———
Schwab, Larry, review by, 186–187
Sciurus aberti, 536
spp., 619
Scolopax minor, 686–697
spp., 101, 102
Scopus spp., 100
Scoter, Black, see Melanitta nigra
Screech-Owl, Eastern, see Otus asio
Puerto Rican, see Otus nudipes
Western, see Otus kennicottii
Scythrops spp., 102
Searcy, William A., review by, 393–394
Secretary-bird, see Sagittarius serpentarius
Seginak, John T., see Krementz, David G., ———, and Grey W. Pendleton
Seiurus aurocapillus, 26–39, 169–174, 368, 369, 580
noveboracensis, 580, 581, 582, 587, 765
Selasphorus platycercus, 468, 469, 720
Semioptera wallacii, 371–373
Serinus spp., 103
Setophaga ruticilla, 26–39, 368, 577–589
Seutin, Gilles, and Victor Apanius, Gray Flycatcher predation on a hummingbird, 565–567
sex ratio
in migrating Calidris minutilla in British Columbia, 413–422
shad, see Dorosoma sp.
Shearwater, Short-tailed, see Puffinus tenuirostris
Sooty, see Puffinus griseus
Townsend's, see Puffinus auricularis
sheep, see Ovis aries
shiner, golden, see Notemigonus crysoleucas
Shoveler, Northern, see Anas clypeata
Shrike, Great Gray, see Lanius excubitor
Lesser Grey, see Lanius minor
Loggerhead, see Lanius ludovicianus
Woodchat, see Lanius senator
Sialia mexicana, 721, 722
sialis, 125, 127, 129, 289–295, 377–379, 701, 702
Siskin, Pine, see Carduelis pinus
Sitta canadensis, 125, 127, 129, 468, 720
carolinensis, 122–130, 701, 702, 704, 705, 721
pusilla, 542–547
pygmaea, 720
Skua, Brown, see Catharacta lonnbergi
South Polar, see Catharacta maccormicki
skunk, hog-nosed, see Conepatus chinga
striped, see Mephitis mephitis
Skylark, Oriental, see Alauda gulgula
Small, Arnold, California birds: their status and distribution, reviewed, 571–572
Smith, Jeff P., Foraging sociability of nesting wading birds (Ciconiiformes) at Lake Okeechobee, Florida, 437–451
snake, climbing rat, see Elaphe obsoleta
gopher, see Pituophis melanoleucus
mangrove water, see Nerodia compressicauda
Solenopsis invicta, 761–762
Sparrow, American Tree, see Spizella arborea
Baird's, see Ammodramus bairdii
Black-throated, see Amphispiza bilineata
Black-chinned, see Spizella atrogularis
Brewer's, see Spizella breweri
Chipping, see Spizella passerina
Clay-colored, see Spizella pallida
Field, see Spizella pusilla
Fox, see Passerella iliaca
Golden-crowned, see Zonotrichia atricapilla
Grasshopper, see Ammodramus savannarum
House, see Passer domesticus
"Lesser Field", see Passer agrestis
Lincoln's, see Melospiza lincolnii
Rufous-crowned, see Aimophila ruficeps
Savannah, see Passerculus sandwichensis
Song, see Melospiza melodia
Timberline, see Spizella taverni
Vesper, see Pooecetes gramineus
White-crowned, see Zonotrichia leucophrys
White-throated, see Zonotrichia albicollis
White-throated × Dark-eyed Junco, see Zonotrichia albicollis × Junco hyemalis
Worthen's see Spizella wortheni
species nova
Glaucidium parkeri, 1–6
species richness

in relation to isolation in aspen habitat, 463–474
Speotyto cunicularia, 765
Spermophilus spp., 254, 262, 619
variegatus, 262
Spheniscus demersus, 94
spp., 98
Sphyrapicus nuchalis, 464, 468, 471, 749
varius, 746–752
Spilornis cheela, 97
spp., 100
Spiza americana, 709–718
Spizella arborea, 126, 128, 129, 641–654
atrogularis, 641–654
breweri, 641–654
pallida, 641–654, 709–718
passerina, 641–654
pusilla, 126, 128, 129, 193–213 (Frontispiece), 641–654
taverneri, 650
wortheni, 650
squirrel, Abert's, see Sciurus aberti
ground, see Spermophilus sp.
red, see Tamiasciurus grahamensis
rock, see Spermophilus variegatus
Starling, European, see Sturnus vulgaris
Steatornis spp., 103
Stenzel, Lynne E., see Warnock, Nils, Gary W. Page, and ———
Stercorarius spp., 102
Sterna albifrons, 767
hirundo, 423–436
spp., 102
Stevenson, Henry M., and Bruce H. Anderson, The birdlife of Florida, reviewed, 574
Stictonetta naevosa, 217
Stilt, Banded, see Cladorhynchus leucocephalus
Black-winged, see Himantopus himantopus
Stint, Rufous-necked, see Calidris ruficollis
Stork, Wood, see Mycteria americana
Storm-petrel, Fork-tailed, see Oceanodroma furcata
Leach's, see Oceanodroma leucorhoa
Streptopelia decaocto, 97
spp., 102
Strigops spp., 102, 110
Strix aluco, 536
occidentalis, 721 (Frontispiece)
occidentalis caurina, 604
spp., 103
Struthio spp., 97
Sturnella loica, 679
magna, 127, 129
neglecta, 709–718
Sturnus vulgaris, 122–130, 165–169, 306–316, 382
sucker, desert, see Catostomus clarkii
Sonora, see Catostomus insignis
Sula spp., 100
Sunbittern, see Eurypyga helias
sunfish, see Lepomis spp.
Swallow, Cliff, see Hirundo pyrrhonota
Tree, see Tachycineta bicolor
Violet-green, see Tachycineta thalassina
Sylvia borin, 297, 301
Sylvilagus audubonii, 261, 262
bachmani, 254
Syrrhaptes spp., 102
systematics
review of avian cecum, 93–121
Tachybaptus ruficollis, 94
spp., 98
Tachycineta bicolor, 42, 153–164, 294, 378, 468, 471
thalassina, 262, 720
Taeniopygia guttata, 763
Takahe, New Zealand, see Notornis mantelli
Tamias spp., 619
striatus, 170
Tamiasciurus grahamensis, 719*
Tanager, Hepatic, see Piranga flava
Scarlet, see Piranga olivacea
Summer, see Piranga rubra
Western, see Piranga ludoviciana
Tauraco spp., 102
taxonomy
Anas platyrhynchos-like ducks, 548–551
Glaucidium minutissimum complex, 7–25
of stiff-tailed ducks (Anatidae: Oxyurini), 214–234
Tayassu tajacu, 262
Teal, Blue-winged, see Anas discors
Cinnamon, see Anas cyanoptera
Cotton, see Nettapus coromandelianus
Green-winged, see Anas crecca
Tedford, Bruce L., see Marra, Peter P., Kevin T. Lampe, and ———

Temby, I. D., see Emison, W. B., C. M. Beardsell, and ———
Tern, Common, see Sterna hirundo
Little, see Sterna albifrons
Terranova, Estaban, see Latta, Steven C., Joseph M. Wunderle, Jr., ———, and Michelle Pagán
Tetrao urogallus, 108
Thalassornis leuconotus, 214
Theristicus caudatus, 679
Thibault, Michel, and Raymond McNeil, Predator-prey relationship between Wilson's Plovers and fiddler crabs in northeastern Venezuela, 73–80
Thinocorus spp., 102
Thomlinson, John R., Landscape characteristics associated with active and abandoned Red-cockaded Woodpecker clusters in east Texas, 603–614
Thompson, Jonathan E., and Ronald D. Drobney, Intensity and chronology of postreproductive molts in male Canvasbacks, 338–358
Thomson, Tom, Birding in Ohio, reviewed, 572–573
Thrasher, Brown, see Toxostoma rufum
Pearly-eyed, see Margarops fuscatus
Thrush, Hermit, see Catharus guttatus
Swainson's, see Catharus ustulatus
Wood, see Hylocichla mustelina
Thryomanes bewickii, 721
Thryothorus ludovicianus, 122–130, 701, 702, 704, 705
Tinamou, Brushland, see Nothoprocta cinerascens
Elegant Crested, see Eudromia elegans
Small-billed, see Crypturellus parvirostris
Spotted, see Nothura maculosa
Tinamus spp., 98
Titmouse, Bridled, see Parus wollweberi
Tufted, see Parus bicolor
Tityra, Masked, see Tityra semifasciata
Tityra semifasciata, 19, 374
Todus mexicanus, 103, 181–182
Tody, Puerto Rican, see Todus mexicanus
Towhee, Abert's, see Pipilo aberti
California, see Pipilo crissalis
Canyon, see Pipilo fuscus
Collared, see Pipilo ocai
Green-tailed, see Pipilo chlorurus
Rufous-sided, see Pipilo erythrophthalmus
White-throated, see Pipilo albicollis
Toxostoma rufum, 44, 701, 702
spp., 552
Tragopan, Satyr, see Tragopan satyra
Tragopan satyra, 101
Travani, Alejandro, see Hiraldo, Fernando, José A. Donázar, Olga Ceballos, ———, Javier Bustamante, and Martín Funes
Tricholomnas spp., 101
Tringa melanoleuca, 131
nebularia, 132
totanus, 131
Trionyx spiniferus, 261
Trivelpiece, Wayne, see Emslie, Steven D., Nina Karnovsky, and ———
Troglodytes aedon, 51, 468, 471, 701, 702, 704 705, 721 (Frontispiece)
Trogon spp., 103
Turchi, Gail M., Patricia L. Kennedy, Dean Urban, and Dale Hein, Bird species richness in relation to isolation of aspen habitat, 463–474
Turdus falcklandii, 679
grayi, 375
migratorius, 44, 51, 125, 127, 129, 378, 468, 702, 720
spp., 103
Turkey, Wild, see Meleagris gallopavo
Turnix spp., 101
Turnstone, Ruddy, see Arenaria interpres
turtle, Sonora mud, see Kinosternon sonoriense
spiny softshell, see Trionyx spiniferus
Tympanuchus cupido attwateri, 761
Tyrannus dominicensis, 565–567
Tyto alba, 102
spp., 103
Upupa spp., 103
Urban, Dean, see Turchi, Gail M., Patricia L. Kennedy, ———, and Dale Hein
Urban, Emil K., see Keith, Stuart, ———, and C. Hilary Fry
Uria aalge, 321, 325, 326, 397–412
lomvia, 397–412
spp., 102
Urocyon cinereoargenteus, 170
Valburg, Ray, see Marr, N. Vern, W. Dan-

iel Edge, Robert G. Anthony, and ———
Vanellus chilensis, 679
indicus, 97
spp., 102
vanellus, 131
Veit, Richard R., and Wayne R. Petersen, Birds of Massachusetts, reviewed, 391
Vermivora celata, 721, 722 (Frontispiece)
chrysoptera, 579
peregrina, 374
pinus, 579
virginiae, 720
Vireo flavifrons, 44, 48, 374, 582
gilvus, 464, 468, 469, 720
griseus, 26–39, 44
huttoni, 721
olivaceus, 26–39, 368, 369
solitarius, 720
Vireo, Hutton's see Vireo huttoni
Red-eyed, see Vireo olivaceus
Solitary, see Vireo solitarius
Warbling, see Vireo gilvus
White-eyed, see Vireo griseus
Yellow-throated, see Vireo flavifrons
vocalization
of breeding Lagopus lagopus, 496–509
seasonal response to taped-playback songs in Hylocichla mustelina, 738–741
Vulpes vulpes, 170, 276, 284, 287, 397
Vulture, Turkey, see Cathartes aura
Wagtail, Gray, see Motacilla cinerea
Warbler, Adelaide's, see Dendroica adelaidae
Arrow-headed, Warbler, see Dendroica pharetra
Black-and-white, see Mniotilta varia
Black-throated Blue, see Dendroica caerulescens
Black-throated Gray, see Dendroica nigrescens
Blue-winged, see Vermivora pinus
Cape May, see Dendroica tigrina
Garden, see Sylvia borin
Grace's, see Dendroica graciae
Golden-winged, see Vermivora chrysoptera
Hooded, see Wilsonia citrina
Kentucky, see Oporornis formosus
Kirtland's, see Dendroica kirtlandii
Magnolia, see Dendroica magnolia
MacGillivray's, see Oporornis tolmiei
Olive, see Peucedramus taeniatus
Olive-capped, see Dendroica pityophila
Orange-crowned, see Vermivora celata
Palm, see Dendroica palmarum
Pine, see Dendroica pinus
Plumbeous, see Dendroica plumbea
Prairie, Dendroica discolor
Prothonotary, see Protonotaria citrea
Red-faced, see Cardellina rubrifrons
Tennessee, see Vermivora peregrina
Virginia's, see Vermivora virginiae
Vitelline, see Dendroica vitellena
Wilson's, see Wilsonia pusilla
Worm-eating, see Helmitheros vermivorus
Yellow, see Dendroica petechia
Yellow-rumped, see Dendroica coronata
Warkentin, Ian G., and Eugene S. Morton, Roosting behavior of Prothonotary Warblers in non-breeding season, 374–376
Warnock, Nils, Gary W. Page, and Lynne E. Stenzel, Non-migratory movements of Dunlins on their California wintering grounds, 131–139
Waterthrush, Northern, see Seiurus noveboracensis
Watts, Bryan D., and Dana S. Bradshaw, Ghost crab preys on Piping Plover eggs, 767–768
Waxwing, Bohemian, see Bombycilla garrulus
Cedar, see Bombycilla cedrorum
Webb, Sophie W., see McCallum, D. Archibald, Frederick R. Gehlbach, and ———
Weller, Milton W., review by, 187–188
wetland
use by breeding and postbreeding Anas platyrhynchos, 55–63
Whaley, Wayne H., and Clayton M. White, Trends in geographic variation of Cooper's Hawk and Northern Goshawk in North America: a multivariate analysis, reviewed, 770–771
Whimbrel, see Numenius phaeopus
Whip-poor-will, see Caprimulgus vociferus
White, Clayton M., review by, 188–189

White, Clayton M., see Whaley, Wayne H., and ———
Wigeon, American, see Anas americana
Willet, see Catoptrophorus semipalmatus
Wilson, Karen A., Rebecca Field, and Marcia H. Wilson, Successful nesting behavior of Puerto Rican Parrots, 518–529
Wilson, Marcia H., see Wilson, Karen A., Rebecca Field, and ———
Wilsonia citrina, 26–39, 153
  pusilla, 26–39, 582
Winker, Kevin, Habitat selection in woodland Nearctic-Neotropical migrants on the isthmus of Tehuantepec I. Autumn migration, 26–39
Winkler, Raffael, see Jenni, Lukas, and ———
wintering grounds
  movements of Calidris alpina, 131–139
Wood-Pewee, Western, see Contopus sordidulus
Woodhoopoe, Green, see Phaeniculus purpureus
Woodpecker, Acorn, see Melanerpes formicivorus
  Downy, see Picoides pubescens
  Eurasian Green, see Picus viridis
  Gila, see Melanerpes uropygialis
  Hairy, see Picoides villosus
  Pileated, see Dryocopus pileatus
  Red-bellied, see Melanerpes carolinus
  Red-cockaded, see Picoides borealis
  Strickland's [Arizona], see Picoides stricklandi
woodrat, see Neotoma spp.
Woods, Christopher P., Food delivery and food holding during copulation in the Loggerhead Shrike, 762–764
Wren, Bewick's, see Thryomanes bewickii
  Cactus, see Campylorhynchus brunneicapillus
  Canyon, see Catherpes mexicanus
  Carolina, see Thryothorus ludovicianus
  House [Brown-throated], see Troglodytes aedon
  Sedge, see Cistothorus platensis
Wunderle, Joseph M., Jr., see Latta, Steven C., ———, Esteban Terranova, and Michelle Pagán
Xanthocephalus xanthocephalus, 386
Yahner, Richard H., and Bradley D. Ross, Seasonal response of Wood Thrushes to taped-playback songs, 738–741
Yahner, Richard H., Habitat use by wintering and breeding bird communities in relation to edge in an irrigated forest, 365–371
Yaukey, Peter H., Effects of food supplementation and predator simulation on nuthatches and parids within mixed-species flocks, 542–547
Yellowleg, Greater, see Tringa melanoleuca
Yellowthroat, Common, see Geothlypis trichas
Zaedyus pichiy, 679
Zeller, Nanette S., and Jaime A. Collazo, Abundance and distribution of overwintering passerines in bottomland hardwood forests in North Carolina, 698–708
Zenaida asiatica, 262
  auriculata, 679
  aurita, 460
  macroura, 126, 128, 129, 262, 709–718
Zink, Robert M., see Dodge, Anthony G., Adam J. Fry, Rachelle C. Blackwell, and ———
Zonotrichia albicollis, 125, 127, 129, 193–213, 296–305, 367, 369, 701, 702, 723–727
  albicollis × Junco hyemalis, 193–213
  atricapilla, 651
  leucophrys, 127, 129, 179–181, 296–305, 540

This issue of *The Wilson Bulletin* was published on 27 December 1995.

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOLUME 107 1995 QUARTERLY

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DATES OF ISSUE OF VOLUME 107
OF THE WILSON BULLETIN

NO. 1—8 MARCH 1995
NO. 2—2 JUNE 1995
NO. 3—1 SEPTEMBER 1995
NO. 4—27 DECEMBER 1995

CONTENTS OF VOLUME 107

NUMBER 1

MAJOR PAPERS

A NEW SPECIES OF PYGMY-OWL (STRIGIDAE: *GLAUCIDIUM*) FROM THE EASTERN ANDES ..... *Mark B. Robbins and Steve N. G. Howell* 1

SPECIES LIMITS OF THE LEAST PYGMY-OWL (*GLAUCIDIUM MINUTISSIMUM*) COMPLEX ..... *Steve N. G. Howell and Mark B. Robbins* 7

HABITAT SELECTION IN WOODLAND NEARCTIC–NEOTROPIC MIGRANTS ON THE ISTHMUS OF TEHUANTEPEC I. AUTUMN MIGRATION ..... *Kevin Winker* 26

A COMPARISON OF BIRD COMMUNITIES IN BURNED AND SALVAGE-LOGGED, CLEARCUT, AND FORESTED FLORIDA SAND PINE SCRUB ..... *Cathryn H. Greenberg, Lawrence D. Harris, and Daniel G. Neary* 40

WETLAND USE BY BREEDING AND POSTBREEDING FEMALE MALLARDS IN THE ST. LAWRENCE RIVER VALLEY ..... *Michael P. Losito and Guy A. Baldassarre* 55

SPRING FEEDING ECOLOGY OF CINNAMON TEAL IN ARIZONA ..... *James H. Gammonley* 64

PREDATOR-PREY RELATIONSHIP BETWEEN WILSON'S PLOVERS AND FIDDLER CRABS IN NORTHEASTERN VENEZUELA ..... *Michel Thibault and Raymond McNeil* 73

LOSSES OF RED-COCKADED WOODPECKER CAVITY TREES TO SOUTHERN PINE BEETLES ..... *Richard N. Conner and D. Craig Rudolph* 81

THE AVIAN CECUM: A REVIEW ..... *Mary H. Clench and John R. Mathias* 93

BIAS IN CHRISTMAS BIRD COUNTS FOR SPECIES THAT VISIT FEEDERS ..... *Erica H. Dunn* 122

NON-MIGRATORY MOVEMENTS OF DUNLINS ON THEIR CALIFORNIA WINTERING GROUNDS ..... *Nils Warnock, Gary W. Page, and Lynne E. Stenzel* 131

INVESTIGATOR DISTURBANCE, CHICK MOVEMENT, AND AGGRESSIVE BEHAVIOR IN RING-BILLED GULLS ..... *Kevin M. Brown and Ralph D. Morris* 140

A TEST OF AN ASSUMPTION OF DELAYED PLUMAGE MATURATION HYPOTHESES USING FEMALE TREE SWALLOWS ..... *George A. Lozano and Paul T. Handford* 153

SHORT COMMUNICATIONS

CAPSAICIN DETECTION IN TRAINED EUROPEAN STARLINGS: THE IMPORTANCE OF OLFACTION AND TRIGEMINAL CHEMORECEPTION ..... *J. Russell Mason and Larry Clark* 165

DEPREDATION OF ARTIFICIAL OVENBIRD NESTS IN A FOREST PATCH ..... *Eric T. Linder and Eric K. Bollinger* 169

DIET OF NESTING KILLDEER IN NORTH DAKOTA ..... *Jeanne M. Fair, Patricia L. Kennedy, and Lowell C. McEwen* 174

UNUSUAL MARBLED MURRELET NEST ..... *Cheri Ford and Mike Brown* 178

THE PARASITIC BLOW FLY, *PROTOCALLIPHORA SPATULATA*, IN TWO NEW HOST SPECIES ..... *Jeanne M. Fair and Clinton K. Miller* 179

FRUIT IN THE DIET OF NESTLINGS OF THE PUERTO RICAN TODY, A TROPICAL INSECTIVORE ..... *Michele Merola* 181

NOTES ON THE NESTING BEHAVIOR OF THE WHITE-BELLIED WOODPECKER ..... *A. Townsend Peterson, Nina Ingle, and Renato Fernandez* 182

ORNITHOLOGICAL LITERATURE 185

NUMBER 2

MAJOR PAPERS

HISTORIC AND TAXONOMIC IMPLICATIONS OF RECENTLY FOUND ARTWORK IN ARITHMETIC BOOKS OF STUDENTS OF ALEXANDER WILSON ..... *Edward H. Burtt, Jr. and William E. Davis, Jr.* 193

PHYLOGENY AND COMPARATIVE ECOLOGY OF STIFF-TAILED DUCKS (ANATIDAE: OXYURINI) ..... *Bradley C. Livezey* 214

MORPHOLOGICAL AND GENETIC DIVERGENCE AMONG ALASKAN POPULATIONS OF *BRACHYRAMPHUS* MURRELETS ..... *Jay Pitocchelli, John Piatt, and Matthew A. Cronin* 235

SHEEP CARCASS AVAILABILITY AND USE BY BALD EAGLES ..... *N. Vern Marr, W. Daniel Edge, Robert G. Anthony, and Ray Valburg* 251

FOOD HABITS OF BALD EAGLES BREEDING IN THE ARIZONA DESERT ..... *Teryl G. Grubb* 258

BREEDING BIOLOGY OF SNOWY PLOVERS AT GREAT SALT LAKE, UTAH ..... *Peter W. C. Paton* 275

EASTERN BLUEBIRDS ARE ATTRACTED TO TWO-BOX SITES ..... *Jonathan H. Plissner and Patricia Adair Gowaty* 289

PLASMA CORTICOSTERONE LEVELS IN TWO SPECIES OF *ZONOTRICHIA* SPARROWS UNDER CAPTIVE AND FREE-LIVING CONDITIONS ..... *Peter P. Marra, Kevin T. Lampe, and Bruce L. Tedford* 296

SOME FACTORS AFFECTING PRECISION OF THE TOTAL BODY ELECTRICAL CONDUCTIVITY TECHNIQUE FOR MEASURING BODY COMPOSITION IN LIVE BIRDS ..... *Andreas Asch and Daniel D. Roby* 306

AVIAN PREDATION AT PENGUIN COLONIES ON KING GEORGE ISLAND, ANTARCTICA ..... *Steven D. Emslie, Nina Karnovsky, and Wayne Trivelpiece* 317

HATCHING, GROWTH, AND MORTALITY OF MAGNIFICENT FRIGATEBIRD CHICKS IN SOUTHERN BAJA CALIFORNIA ..... *Roberto Carmona, Juan Guzmán, and Juan F. Elorduy* 328

INTENSITY AND CHRONOLOGY OF POSTREPRODUCTIVE MOLTS IN MALE CANVASBACKS ..... *Jonathan E. Thompson and Ronald D. Drobney* 338

SHORT COMMUNICATIONS

MOLT CHRONOLOGY OF MALE MALLARDS WINTERING IN MISSOURI ..... *Daniel L. Combs and Leigh H. Fredrickson* 359

HABITAT USE BY WINTERING AND BREEDING BIRD COMMUNITIES IN RELATION TO EDGE IN AN IRRIGATED FOREST ..... *Richard H. Yahner* 365

SEQUENCE OF PLUMAGE EVOLUTION IN THE STANDARDWING BIRD OF PARADISE ..... *Gary R. Graves* 371

ROOSTING BEHAVIOR OF PROTHONOTARY WARBLERS IN THE NON-BREEDING SEASON ..... *Ian G. Warkentin and Eugene S. Morton* 374

TIME OF DAY OF EGG LAYING BY EASTERN BLUEBIRDS ..... *Susan B. Meek and Raleigh J. Robertson* 377

SEX-BIASED KLEPTOPARASITISM OF HOODED MERGANSERS BY RING-BILLED GULLS ..... *Felipe Chavez-Ramirez* 379

INTRASPECIFIC VARIATION IN EGG COMPOSITION ..... *Wendy L. Hill* 382

ORNITHOLOGICAL LITERATURE 388

NUMBER 3

MAJOR PAPERS

ARTIC FOX INFLUENCE ON A SEABIRD COMMUNITY IN LABRADOR: A NATURAL EXPERIMENT ..... *T. R. Birkhead and D. N. Nettleship* 397

MIGRATION CHRONOLOGY, SEX RATIO, AND BODY MASS OF LEAST SANDPIPERS IN BRITISH COLUMBIA ..... *Robert W. Butler and Gary W. Kaiser* 413

COMMON TERNS NESTING ON NAVIGATIONAL AIDS AND NATURAL ISLANDS IN THE ST. LAWRENCE RIVER, NEW YORK ..... *Kenneth Karwowski, J. Edward Gates, and Lee H. Harper* 423

FORAGING SOCIABILITY OF NESTING WADING BIRDS (CICONIIFORMES) AT LAKE OKEECHOBEE, FLORIDA ..... *Jeff P. Smith* 437

DISTRIBUTION AND ABUNDANCE OF RAPTORS IN PUERTO RICO ..... *Frank F. Rivera-Milán* 452

BIRD SPECIES RICHNESS IN RELATION TO ISOLATION OF ASPEN HABITATS ..... *Gail M. Turchi, Patricia L. Kennedy, Dean Urban, and Dale Hein* 463

BREEDING BIOLOGY OF FLORIDA PRAIRIE WARBLERS AND CUBAN YELLOW WARBLERS ..... *John W. Prather and Alexander Cruz* 475

ARTHROPOD PREY OF NESTLING RED-COCKADED WOODPECKERS IN THE UPPER COASTAL PLAIN OF SOUTH CAROLINA ..... *James L. Hanula and Kathleen E. Fanzreb* 485

THE CALLS AND ASSOCIATED BEHAVIOR OF BREEDING WILLOW PTARMIGAN IN CANADA ..... *Kathy Martin, Andrew G. Horn, and Susan J. Hannon* 496

NATURAL HISTORY OF THE MONK PARAKEET IN HYDE PARK, CHICAGO ..... *Jeremy Hyman and Stephen Pruett-Jones* 510

SUCCESSFUL NESTING BEHAVIOR OF PUERTO RICAN PARROTS ..... *Karen A. Wilson, Rebecca Field, and Marcia H. Wilson* 518

LIFE HISTORY AND ECOLOGY OF FLAMMULATED OWLS IN A MARGINAL NEW MEXICO POPULATION ..... *D. Archibald McCallum, Frederick R. Gehlbach, and Sophie W. Webb* 530

SHORT COMMUNICATIONS

THE EFFECTS OF EXOGENOUS TESTOSTERONE ON MALE NORTHERN MOCKINGBIRDS DURING THE BREEDING SEASON ..... *Michael J. Justice and Cheryl A. Logan* 538

EFFECTS OF FOOD SUPPLEMENTATION AND PREDATOR SIMULATION ON NUTHATCHES AND PARIDS WITHIN MIXED-SPECIES FLOCKS ..... *Peter H. Yaukey* 542

MALLARD-LIKE DUCKS IN THE PLAYA LAKES REGION ..... *Alan M. Fedynich and Olin E. Rhodes, Jr.* 548

FIRST DESCRIPTION OF THE NEST AND EGGS OF THE SOCORRO MOCKINGBIRD ..... *Juan E. Martínez Gómez and Robert L. Curry* 551

EXCEPTIONAL RESPONSE BY FEMALE RED CROSSBILLS TO DIETARY CAROTENOID SUPPLEMENTATION ..... *Geoffrey E. Hill and Craig W. Benkman* 555

WINTER FOOD OF A SMALL INSECTIVOROUS BIRD, THE GOLDEN-CROWNED KINGLET ..... *Bernd Heinrich and Ross Bell* 558

FIRST NESTING RECORD OF THE GREAT-TAILED GRACKLE IN OREGON ..... *Eric J. Scheuering and Gary L. Ivey* 562

GROUND-NESTING LONG-EARED OWLS ..... *Michael T. Maples, Denver W. Holt, and R. Wayne Campbell* 563

GRAY FLYCATCHER PREDATION ON A HUMMINGBIRD ..... *Gilles Seutin and Victor Apanius* 565

ORNITHOLOGICAL LITERATURE 568

NUMBER 4

MAJOR PAPERS

NEOTROPICAL MIGRANTS IN UNDISTURBED AND HUMAN-ALTERED FORESTS OF JAMAICA ..... *John L. Confer and Richard T. Holmes* 577

AN EXPERIMENTAL STUDY OF NEST PREDATION IN A SUBTROPICAL WET FOREST FOLLOWING HURRICANE DISTURBANCE ..... *Steven C. Latta, Joseph M. Wunderle, Jr., Esteban Terranova, and Michelle Pagán* 590

LANDSCAPE CHARACTERISTICS ASSOCIATED WITH ACTIVE AND ABANDONED RED-COCKADED WOODPECKER CLUSTERS IN EAST TEXAS ..... *John R. Thomlinson* 603

ARE RED-TAILED HAWKS AND GREAT HORNED OWLS DIURNAL-NOCTURNAL DIETARY COUNTERPARTS? ..... *Carl D. Marti and Michael N. Kochert* 615

FEEDING BEHAVIOR, PREY SELECTION, AND BILL SIZE OF PIED AND SOOTY OYSTERCATCHERS IN AUSTRALIA ..... *Brook Lauro and Erica Nol* 629

COMPARISON OF PHYLOGENIES DERIVED FROM TWO MOLECULAR DATA SETS IN THE AVIAN GENERA *PIPILO* and *SPIZELLA* ..... *Anthony G. Dodge, Adam J. Fry, Rachelle C. Blackwell, and Robert M. Zink* 641

WITHIN-SEASON TRENDS IN THE FORAGING BEHAVIOR OF THE MOUNTAIN CHICKADEE ..... *Paula K. Kleintjes and Donald L. Dahlsten* 655

DEMOGRAPHICS OF A DECLINING FLOCK OF GREATER SANDHILL CRANES IN OREGON ..... *Carroll D. Littlefield* 667

BREEDING BIOLOGY OF A GREY EAGLE-BUZZARD POPULATION IN PATAGONIA ..... *Fernando Hiraldo, José A. Donázar, Olga Ceballos, Alejandro Travaini, Javier Bustamante, and Martín Funes* 675

HABITAT USE AT NIGHT BY WINTERING AMERICAN WOODCOCK IN COASTAL GEORGIA AND VIRGINIA ..... *David G. Krementz, John T. Seginak, and Grey W. Pendleton* 686

ABUNDANCE AND DISTRIBUTION OF OVERWINTERING PASSERINES IN BOTTOMLAND HARDWOOD FORESTS IN NORTH CAROLINA ..... *Nanette S. Zeller and Jaime A. Collazo* 698

CONTRIBUTIONS OF THE CONSERVATION RESERVE PROGRAM TO POPULATIONS OF BREEDING BIRDS IN NORTH DAKOTA ..... *Douglas H. Johnson and Lawrence D. Igl* 709

SHORT COMMUNICATIONS

BIRDS OF CONIFEROUS FOREST ON MOUNT GRAHAM, ARIZONA ..... *Joe T. Marshall* 719

SEASONAL AND DIURNAL MASS VARIATION IN BLACK-CAPPED CHICKADEES AND WHITE-THROATED SPARROWS ..... *Susannah K. Graedel and Robert E. Loveland* 723

DETECTABILITY AND POPULATION DENSITY OF SCALY-NAPED PIGEONS BEFORE AND AFTER HURRICANE HUGO IN PUERTO RICO AND VIEQUES ISLAND ..... *Frank F. Rivera-Milán* 727

BOTFLY ECTOPARASITISM OF THE BROWN CACHOLOTE AND THE FIREWOOD-GATHERER ..... *Ana I. Nores* 734

SEASONAL RESPONSE OF WOOD THRUSHES TO TAPED-PLAYBACK SONGS ..... *Richard H. Yahner and Bradley D. Ross* 738

EFFECTS OF LAYING DATE, CLUTCH SIZE, AND COMMUNAL NEST SIZE ON THE REPRODUCTIVE SUCCESS OF MONK PARAKEETS ..... *Joaquín L. Navarro, Mónica B. Martella, and Enrique H. Bucher* 742

THE INFLUENCE OF YELLOW-BELLIED SAPSUCKERS ON LOCAL INSECT COMMUNITY STRUCTURE ..... *Leslie J. Rissler, David N. Karowe, Francesca Cuthbert, and Brian Scholtens* 746

DIURNAL ACTIVITY BUDGETS OF PRE-NESTING SANDHILL CRANES IN ARCTIC CANADA ..... *Anthony D. Fox, Hugh Boyd, and Robert G. Bromley* 752

MATE GUARDING TACTICS USED BY GREAT CRESTED FLYCATCHERS ..... *Elizabeth A. MacDougall-Shackleton and Raleigh J. Robertson* 757

RED IMPORTED FIRE ANT PREDATION ON CRESTED CARACARA NESTLINGS IN SOUTH TEXAS ..... *Vanessa M. Dickinson* 761

FOOD DELIVERY AND FOOD HOLDING DURING COPULATION IN THE LOGGERHEAD SHRIKE ..... *Christopher P. Woods* 762

ADDITIONAL RECORDS OF OWLS AND WOOD WARBLERS FROM MEXICO ..... *Armando J. Contreras-Balderas, Juan A. García-Salas, and Jose I. Gonzáles-Rojas* 765

AN UNUSUAL RECORD OF SANDHILL CRANE PHILOPATRY ..... *Carroll D. Littlefield and Gary L. Ivey* 766
GHOST CRAB PREYS ON PIPING PLOVER EGGS ..... *Bryan D. Watts and Dana S. Bradshaw* 767
GHOST CRAB PREYS ON A PIPING PLOVER CHICK ..... *John P. Loegering, James D. Fraser, and Lisa L. Loegering* 768
ORNITHOLOGICAL LITERATURE 770
PROCEEDINGS OF THE SEVENTY-SIXTH ANNUAL MEETING ..... *John L. Zimmerman* 776
INDEX ..... *Kathleen G. Beal* 790

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CONTENTS

MAJOR PAPERS

NEOTROPICAL MIGRANTS IN UNDISTURBED AND HUMAN-ALTERED FORESTS OF JAMAICA ..... *John L. Confer and Richard T. Holmes* 577

AN EXPERIMENTAL STUDY OF NEST PREDATION IN A SUBTROPICAL WET FOREST FOLLOWING HURRICANE DISTURBANCE ..... *Steven C. Latta, Joseph M. Wunderle, Jr., Esteban Terranova, and Michelle Pagán* 590

LANDSCAPE CHARACTERISTICS ASSOCIATED WITH ACTIVE AND ABANDONED RED-COCKADED WOODPECKER CLUSTERS IN EAST TEXAS ..... *John R. Thomlinson* 603

ARE RED-TAILED HAWKS AND GREAT HORNED OWLS DIURNAL-NOCTURNAL DIETARY COUNTERPARTS? ..... *Carl D. Marti and Michael N. Kochert* 615

FEEDING BEHAVIOR, PREY SELECTION, AND BILL SIZE OF PIED AND SOOTY OYSTERCATCHERS IN AUSTRALIA ..... *Brook Lauro and Erica Nol* 629

COMPARISON OF PHYLOGENIES DERIVED FROM TWO MOLECULAR DATA SETS IN THE AVIAN GENERA *PIPILO* and *SPIZELLA* ..... *Anthony G. Dodge, Adam J. Fry, Rachelle C. Blackwell, and Robert M. Zink* 641

WITHIN-SEASON TRENDS IN THE FORAGING BEHAVIOR OF THE MOUNTAIN CHICKADEE ..... *Paula K. Kleintjes and Donald L. Dahlsten* 655

DEMOGRAPHICS OF A DECLINING FLOCK OF GREATER SANDHILL CRANES IN OREGON ..... *Carroll D. Littlefield* 667

BREEDING BIOLOGY OF A GREY EAGLE-BUZZARD POPULATION IN PATAGONIA ..... *Fernando Hiraldo, José A. Donázar, Olga Ceballos, Alejandro Travaini, Javier Bustamante, and Martín Funes* 675

HABITAT USE AT NIGHT BY WINTERING AMERICAN WOODCOCK IN COASTAL GEORGIA AND VIRGINIA ..... *David G. Krementz, John T. Seginak, and Grey W. Pendleton* 686

ABUNDANCE AND DISTRIBUTION OF OVERWINTERING PASSERINES IN BOTTOMLAND HARDWOOD FORESTS IN NORTH CAROLINA ..... *Nanette S. Zeller and Jaime A. Collazo* 698

CONTRIBUTIONS OF THE CONSERVATION RESERVE PROGRAM TO POPULATIONS OF BREEDING BIRDS IN NORTH DAKOTA ..... *Douglas H. Johnson and Lawrence D. Igl* 709

SHORT COMMUNICATIONS

BIRDS OF CONIFEROUS FOREST ON MOUNT GRAHAM, ARIZONA ..... *Joe T. Marshall* 719

SEASONAL AND DIURNAL MASS VARIATION IN BLACK-CAPPED CHICKADEES AND WHITE-THROATED SPARROWS ..... *Susannah K. Graedel and Robert E. Loveland* 723

DETECTABILITY AND POPULATION DENSITY OF SCALY-NAPED PIGEONS BEFORE AND AFTER HURRICANE HUGO IN PUERTO RICO AND VIEQUES ISLAND ..... *Frank F. Rivera-Milán* 727

BOTFLY ECTOPARASITISM OF THE BROWN CACHOLOTE AND THE FIREWOOD-GATHERER ..... *Ana I. Nores* 734

SEASONAL RESPONSE OF WOOD THRUSHES TO TAPED-PLAYBACK SONGS ..... *Richard H. Yahner and Bradley D. Ross* 738

EFFECTS OF LAYING DATE, CLUTCH SIZE, AND COMMUNAL NEST SIZE ON THE REPRODUCTIVE SUCCESS OF MONK PARAKEETS ..... *Joaquín L. Navarro, Mónica B. Martella, and Enrique H. Bucher* 742

THE INFLUENCE OF YELLOW-BELLIED SAPSUCKERS ON LOCAL INSECT COMMUNITY STRUCTURE ..... *Leslie J. Rissler, David N. Karowe, Francesca Cuthbert, and Brian Scholtens* 746

DIURNAL ACTIVITY BUDGETS OF PRE-NESTING SANDHILL CRANES IN ARCTIC CANADA ..... *Anthony D. Fox, Hugh Boyd, and Robert G. Bromley* 752

MATE GUARDING TACTICS USED BY GREAT CRESTED FLYCATCHERS ..... *Elizabeth A. MacDougall-Shackleton and Raleigh J. Robertson* 757

RED IMPORTED FIRE ANT PREDATION ON CRESTED CARACARA NESTLINGS IN SOUTH TEXAS ..... *Vanessa M. Dickinson* 761

FOOD DELIVERY AND FOOD HOLDING DURING COPULATION IN THE LOGGERHEAD SHRIKE ..... *Christopher P. Woods* 762

ADDITIONAL RECORDS OF OWLS AND WOOD WARBLERS FROM MEXICO ..... *Armando J. Contreras-Balderas, Juan A. García-Salas, and Jose I. Gonzáles-Rojas* 765

AN UNUSUAL RECORD OF SANDHILL CRANE PHILOPATRY ..... *Carroll D. Littlefield and Gary L. Ivey* 766

GHOST CRAB PREYS ON PIPING PLOVER EGGS ..... *Bryan D. Watts and Dana S. Bradshaw* 767

GHOST CRAB PREYS ON A PIPING PLOVER CHICK ..... *John P. Loegering, James D. Fraser, and Lisa L. Loegering* 768

ORNITHOLOGICAL LITERATURE 770

PROCEEDINGS OF THE SEVENTY-SIXTH ANNUAL MEETING ..... *John L. Zimmerman* 776

INDEX ..... *Kathleen G. Beal* 790

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